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The

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The Ecology and Distribution of Hepaticae in Central and Western New York

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Introduction

Local manuals and lists of liverworts have been appearing in ever increasing frequency during the last two or three decades; much of the northern half of the eastern United States is now covered by these. The work of Evans, Andrews, Steere, Sharp, Blomquist, Underwood, Austin, Sullivant, Porter, Ammons, Fulford and a number of other students has resulted in numerous papers dealing with the occurrence and distribution of Hepaticae in temperate eastern North America. One of the least known regions, in fact a veritable lacuna in our knowledge of hepatic distribution, is the area treated herein. Two very incomplete local lists[1] have appeared, which together with a number of short notes and incidental reports, establish the presence of about fifty species of Hepaticae in our region — some indeed with but slim assurance of

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1 Day (1882) and Goodrich (1912).

any certainty that they really occur. This represents little more than one third of the number of Hepaticae which really have been found, and of which authentic material has been examined from our area.[2]

The relatively large number of species reported (more than given by Ammons (1940) for all of West Virginia and greater than reported by Evans and Nichols (1908) for Connecticut) plus the fact that there is no modern manual which adequately discusses the ecological relationships of the species for North America, should make the present work useful to the student elsewhere as well. With this fact in view, notes aiding recognition are given under the ecological and distribution discussion of each species. In this way, it is hoped that the present study will fill a need left unsatisfied by the work of Frye and Clark (1937-1947). However, the formal descriptions of these authors make any attempt at descriptions superfluous here.

In order to save space, it was felt justifiable to delete the citation of collectors and dates of collection except in the case of those species that are merely frequent or rare; for very common species, merely a list of counties from which collections have been examined, is given. For the same reason the locations of the specimens cited are not given. The pertinent material is either in the collection of the Herbarium of Cornell Universtiy, in that of the New York Botanical Garden (Underwood coll.), in that of Syracuse University, in the collection of Dr. A. L. Andrews, or in that of the writer; relatively few of the specimens cited are located elsewhere. Critical specimens of most of the rarer species will be deposited in the collection of the Sullivant Moss Society. The first set of the writer's duplicates have been deposited in the Herbarium of the University of Minnesota.

As there is no modern handbook of the Hepaticae for the northeastern and northcentral states, it was felt that the inclusion of keys and illustrations integrated as far as possible with the keys, would make the following treatment more useful for a wider variety of students. It is hoped that the numerous figures which have been selected from a large variety of original illustrations, will make the work one which even the amateur will find of use. The scales of drawings have been omitted purposely since the writer finds stating that a drawing is magnified 72x means very little so far as visualizing the specimens is concerned.

It is hoped that the following treatment will be useful to students in the colleges and universities of central and western New York; therefore it was considered advisable to present relatively complete tabulations of the localities at which the various species have been collected. This is especially desirable

2 The present paper was in finished manuscript (April, 1946) when the two papers on the hepatics of Cattaraugus County, by P. Boehner (1941, 1943) first came to my attention. The final list by Boehner (1943) represents a very important contribution and entirely invalidates the above two statements. Most of the data presented by Boehner has been incorporated in the following notes. Further collections of several of the species listed by this author are much needed to fully substantiate their local occurrence. I have not seen most of the material cited by Boehner but simply cite his reports as given in the 1943 paper (except where otherwise indicated).

since some indication of abundance is useful in estimating whether a species occurs near the periphery or near the center of the area treated. Many of the rarer species are scarcely holding their own and in some cases they are disappearing from their past haunts, thus making a full tabulation of collections almost necessary.

Since the appearance of the work by Frye and Clark (1937-1947) a number of important papers have been published by European workers (chiefly Müller, Meylan and Buch). In addition, a number of recent critical works published previous to 1937, were overlooked by Frye and Clark. The inclusion of the observations of these students results in a rather different treatment and at times, use of names different from those in Frye and Clark. These papers are briefly referred to in places where they considerably change current concepts in regard to genera and species.

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History of Hepaticology in Central and Western New York: Collectors

Hepaticae have been collected for more than a century in central and western New York. The first collection I have been able to trace is that of *Ricciocarpus natans* made by Nathan W. Folwell near Ovid, Seneca County, in 1831-1832. Very few records are available from that time to the year 1892. In 1866 Peck recorded *Mannia rupestris* from Havana in Schuyler County, the first record of the species from North America. Sixteen years later (1882) a list of species of Hepaticae from the vicinity of Buffalo which included twenty-four species and varieties of hepatics, was published by David F. Days. About this period William R. Dudley, then Professor of Botany at Cornell University, collected plants intensively in the Cayuga Lake Basin of central New York; the Hepaticae among those collected, are now located in the Herbarium of Stanford University, California. I have been unable to examine this material. Somewhat later (1892-1894) Karl McKay Wiegand, later Professor of Botany at Cornell University, collected Hepaticae rather intensively in Cortland and Tompkins counties and made scattered collections subsequently until about the year 1916. His material has been deposited in the Herbarium of Cornell University and his collections are included in the present report. About the same time and until the first few years of the present century, several of the men associated with Cornell University col-

lected hepatic material in the southern part of the Cayuga Lake basin. This material is deposited in the Herbarium of Cornell University and has been examined. Chief among these collectors were Rowlee, Atkinson, Durand, Jackson, and Cipperley.

Since that time but a very few sporadic records have been made of Hepaticae, with the following exceptions:

Shortly subsequent to this period Professor A. L. Andrews of the German Department of Cornell University, began his study of the bryophytes of the Cayuga Lake Basin. He accumulated a considerable number of records of species not found by other collectors and has kindly placed his records at my disposal. In 1910 Evans noted that *Lophozia badensis* had been collected near Ithaca by Dr. Andrews. In 1912 appeared a list of Hepaticae contained in *A Flora of Onondaga County* by Goodrich. This was a very questionable contribution, considering the numerous errors, and records that are still insufficiently established to make their admittance into any flora justified. In 1912 E. J. Hill recorded *Lepidozia setacea* and *Mylia anomala* from Bergen Swamp in Genesee County; in 1916 Evans cited the exsiccatae number of *Porella platyphylla* from Syracuse, Onondaga County (collected by Underwood and Cook) and also cited *Porella platyphylloidea* from Chittenango and Clarkson (based on specimens collected by D. C. Eaton); in 1917 Evans cited the record of *Riccia frostii* from Genesee Falls, Rochester, Monroe County, (collected by P. T. Cleve in 1868).

Several numbers of Hepaticae from the Upper Susquehana were also distributed by Barbour during the turn of the century.

Andrews (1926) reported fifteen species of Hepaticae for the McLean Bog region (Tompkins County).

Since this period a few other species were reported from western New York by Knobloch (1934) and Knobloch and Bleekman (1937) and also by Frye and Clark (1937-1947), who reported *Gymnocolea inflata* and *Ptilidium ciliare* from our region; Castle (1925) first reported *Radula obconica* from central New York.

This list exhausts the number of published references the author has been able to locate on the Hepaticae of central and western New York, except for the two very recent valuable contributions by Boehner (1941, 1943) in which a total of eighty-two species are reported for Cattaraugus County. A possible further exception are the exsiccatae of Underwood and Cook, *Hepaticae Americana* (1887-1899), distributed during the last two decades of the last century of which a considerable number were from the Syracuse region, including several very interesting records.

Very probably one or more references have been omitted but every effort has been made to determine what was known of our hepatic flora.

The writer began studying the Hepaticae of New York in 1937. During the last five years he spent a large share of his time in the study of the Hepaticae of central and western New York. Since the summer of 1942 well over 4000 records have accumulated, and exsiccatae, and often slides, have been prepared of all critical and interesting material. In all cases, even of the

most ubiquitous species, material has been preserved from at least one or two stations in each county. During the progress of this study a very considerable number of species were added to the known flora of central and western New York, a fair number were added to the hepatic flora of New York, and several species were first recorded in the United States east of the Mississippi. It is hoped that the range extensions will be of some interest to the student of biogeography and also that the full tabulation of data regarding distribution, will aid in fixing more exactly the range and frequency of many of our species that occur, in the region treated, at or near their southernmost borders in the United States.

In this paper, 132 species (and varieties or subspecies previously treated as species elsewhere) are reported,[3] as well as a few others included in the keys, that are definitely known to occur in the immediately surrounding region (and therefore to be expected in ours). In a few cases sufficient data have accumulated and enough critical study, especially of poorly known forms, has been carried through, as to contribute materially to our knowledge of several of the species. Some of this data is presented herein.

Taxonomic Treatment

KEY TO THE ORDERS AND SUBORDERS

1 Gametophyte (the green, persistent generation, or "plant") thalloid or leafy, but always with numerous small chloroplasts in each of the vegetative cells. Sporophytes ("fruiting" structures) with a spherical, ovoid, or ellipsoidal capsule (Pl. 1, fig. 1; Pl. 3, fig. 8; Pl. 11, fig. 6, a), never splitting into two valves,[4] its wall 1-several cells thick, brownish or colorless, lacking stomata; columella absent; spiral elaters present (in our forms); oil-cells (at least of gametophyte) distinct, or oil-bodies in all or most cells 2

2. Gametophyte complex, thalloid, thick and completely opaque, always differentiated into distinct tissues and with air-chambers and more or less distinct pores (Pl. 16, figs. 1-2, 4-6; Pl. 17, figs. 1-3, 6); rhizoids of two types: smooth and pegged; oil-bodies limited in occurrence to specialized, diffusely distributed cells (in which they occur as single, large, spherical bodies) (Pl. 16, fig. 5, o). Sporophyte with a very short (non-exserted) seta, or lacking the seta, the capsule of 1 layer of cells, not opening by four sharply defined valves: occurring either immersed within thallus, or in groups on the under side of stalked archegoniophores (Pl. 16, fig. 4) ..... MARCHANTIALES, p. 622

2. Gametophyte simple, a simple leafy plant, or a delicate, simple, more or less translucent thallus: never with distinct differentiation into specialized tissues, never with air-chambers and pores (Pls. 1-15); rhizoids all smooth; oil-bodies occurring 1-several per cell in most somatic cells, never in specialized cells. Sporophyte with an elongate seta, the sporangium becoming long-exserted, mostly 2-several layers of cells thick, opening by four distinct valves,[4] neither immersed in thallus nor elevated on archegoniophores, occurring singly (Pl. 1, fig. 1; Pl. 15, figs. 1, 2, 7) ..... JUNGERMANNIALES, p. 518

3. Gametophyte leafy (Pls. 1-14); often with a ventral, third row of leaves (Pl. 2, figs. 3, 7, 13; Pl. 10, figs. 10-12); female inflorescence terminating the growth

3 This undoubtedly represents nearly all of the species that actually occur in our area. The additions reported in the Appendix (p. 703) raise the total to 136 species and varieties.

4 In the thallose genera *Moerkia* and *Pallavicinia* frequently with division in only two valves.

of the stem (but sometimes with leafy innovations from below the inflorescence) (Pl. 1, fig. 1, etc.); a perianth (Pl. 1, fig. 1; Pl. 3, fig. 8; Pl. 11, fig. 9) usually present, but sometimes replaced by perigynium ..... Suborder Jungermanninae, p. 518

3. Gametophyte thalloid[5]; never with a median ventral third row of leaves (Pl. 15, figs. 1-10; Pl. 18, fig. 3) female inflorescence dorsal, the sporophyte thus also becoming dorsal, not terminating growth of shoot (Pl. 15, fig. 5) ..... Suborder Metzgerinae, p. 609

1. Gametophyte a subcircular, rosette-like, bright to deep green thallus, without any differentiation into tissues (Pl. 18, figs. 7-8, 12); each cell with a single, large, plate-like chloroplast (visible with a hand-lens). Sporophyte with elongate, cylindrical-tapering, more or less terete capsules, splitting into two distinct valves, (Pl. 18, figs. 7-8, 12) the walls several cells thick, with distinct stomata and large chloroplasts; columella distinct; spiral elaters absent (Pl. 18, figs. 4, 6, 10); oil-cells absent ..... ANTHOCEROTALES, p. 630

Treatment of Species
Jungermanniales

Suborder 1. JUNGERMANNINAE (Jungermanniales Acrogynae)

KEY TO GENERA

1. Leaf-lamina largely or entirely resolved into finger-like to filiform lobes or cilia (Pl. 1, figs. 1-2, 4-5, 7-8); underleaves large, similar to leaves (Pl. 1, figs. 6, 9); leaves transverse or incubous, never succubous 2

2. Leaves 4-lobed, the lobes not further divided (Pl. 1, fig. 1; Pl. 2, figs. 1, 5); underleaves simply 3-4-lobed; small species less than 2 mm wide; bright to fuscous green 3

3. Leaf-segments 2 or more cells wide at base, not filiform and flexuous (Pl. 2, figs. 1, 5); perianth on short ventral branches 4

4. Leaves incubous, 4-lobed about half their length, the lobes many cells wide at base (Pl. 2, fig. 5) ..... *Lepidozia*

4. Leaves transverse, 4-lobed to near base, the lobes 2 cells wide at base (Pl. 2, fig. 1) ..... *Microlepidozia*

3. Leaf-segments 1 cell wide to base, filiform, flexuous (Pl. 1, fig. 1); perianths terminal, terete (Pl. 1, fig. 1); leaves transverse ..... *Blepharostoma*

2. Leaves variously divided into 3-5 lobes, the lobes largely resolved into numerous fine cilia a single cell wide (Pl. 1, figs. 2, 4-5, 7-8); leaves incubous; large species, over 2 mm wide; whitish-green or reddish-brown 5

5. Leaf lamina almost entirely resolved into numerous cilia, scarcely evident (Pl. 1, figs. 8-10); trigones of leaf absent (Pl. 1, fig. 9); very pale, whitish green; regularly 2-3-pinnate (Pl. 1, fig. 10); perianth absent; hygrophytic .... *Trichocolea*

5. Leaf-lamina distinct, 6-25 cells wide at base of dorsal lobe (Pl. 1, figs. 4-5, 7); trigones of leaf-cells large, bulging (Pl. 1, fig. 3); never pale yellowish-green, usually brownish or reddish; perianth present; xerophytic ..... *Ptilidium*

1. Leaf-lamina not deeply divided into lobes or cilia: the leaves either entire, or 2-5-

[5] In *Fossombronia*, superficially annectant between the two suborders, there is a distinct stem and lateral leaf-like structures, but the sporophytes are dorsal in position. The violet rhizoids, pure-green color of the rest of the plant, and very large, thin-walled cells devoid of trigonal thickenings, and occurrence on loamy banks or paths will identify the genus.

lobed for 1/8-1/2 their length, or with fine short marginal teeth, i.e., with more than half of the leaf consisting of unbroken lamina (Pl. 2, figs. 2-4, 6-8; Pl. 3, figs. 2, 7; Pl. 11, fig. 7; etc.) 6

6. Leaves sharply complicate-bilobed: consisting of a dorsal and ventral lobe closely applied to each other (Pl. 12, figs. 1, 7-9; Pl. 14, figs. 1-10), either the dorsal or the ventral the larger, usually with a keel between the two 7

7. Dorsal lobe distinctly smaller than ventral: the plants in dorsal view appearing to be provided with 4 rows of leaves (Pl. 12, figs. 1, 7-9, 12); leaf-margins often more or less denticulate and with the apices of lobes pointed or apiculate (Pl. 13, fig. 9); gemmae mostly present and 1-2-celled, only at leaf-apices (Pl. 12, figs. 2-3, 6; Pl. 13, figs. 4-5); underleaves totally absent and rhizoids scattered all along underside of stem 8

8. Gemmae angulate (Pl. 13, fig. 13); leaf-lobes narrow, oblong-ovate, the dorsal mostly directed to near stem apex and at a wide angle with ventral lobes (Pl. 13, figs. 12, 14); keel of leaves obtuse, rounded except near its apex; perianth strongly plicate, contracted to mouth ..... *Diplophyllum*

8. Gemmae ovoid or elliptical, smooth (Pl. 12, figs. 6, 11); leaf-lobes not oblong-ovate and denticulate, directed in nearly the same direction (or dorsal cordate-heart-shaped) (Pl. 12, figs. 1, 7-8, 12); perianth flattened, wide at the truncate mouth, lacking plicae ..... *Scapania*

7. Dorsal lobe always larger than ventral lobe and hiding the ventral lobe in dorsal view (Pl. 14, figs. 1-10); leaves with margins quite entire, with dorsal lobe never apiculate or sharply pointed; gemmae, if present, many-celled and disciform; rhizoids few, in tufts from bases of underleaves, or from ventral lobes 9

9. Underleaves entirely lacking (Pl. 14, figs. 4, 10) 10

10. Minute species to 0.8 cm long, with leaves ovate-pointed; leaves roughened by projecting papillae from cells (appearing minutely denticulate on margins); ventral lobe inflated (Pl. 14, fig. 10); perianth tuberculate, 5-keeled ..... *Cololejeunea*

10. Large species, mostly 1-6 cm long, with leaves oval to circular, smooth; ventral lobe quadrate or nearly, flat (Pl. 14, fig. 4); perianth horizontal, flattened, wide-mouthed ..... *Radula*

9. Underleaves present and quite distinct (Pl. 14, figs. 1, 3, 5-9) 11

11. Ventral lobe and underleaves similar, entire, ovate-rectangular (Pl. 14, fig. 5), parallel to stem (the stem appearing to have three small, subequal rows of leaves ventrally); ventral lobes free from stem, not inflated; plants large, 2-8 cm long, 1.5-4 mm wide ..... *Porella*

11. Ventral lobe and underleaves dissimilar, the underleaves bilobed or circular (Pl. 14, figs. 1-3, 6-8); ventral lobes almost without exception inflated; plants smaller, 0.5-4 cm long, 0.3-1.5 mm wide 12

12. Underleaves entire, circular (Pl. 14, fig. 6) ..... *Leucolejeunea*

12. Underleaves bilobed (Pl. 14, figs. 1-3, 7-9) 13

13. Ventral lobe distant from stem, directed parallel to it, and at right angles to posterior leaf-margin (Pl. 14, figs. 3, 8-9), usually forming a helmet-shaped sac; perianth flattened, trigonous, horizontal (Pl. 14, fig. 9); plants dark green or reddish brown 14

14. Hygrophytic, on wet rocks; dorsal lobe pointed (Pl. 14, fig. 8); ventral lobe often not inflated; trigones minute or absent; dark green ..... *Jubula*

14. Xerophytic, on bark or dry cliffs; dorsal lobe rounded, ventral

usually inflated (Pl. 14, figs. 3, 8); trigones large, bulging; usually dark reddish-brown ..... *Frullania*

13. Ventral lobe attached to stem at posterior insertion of leaf, at an angle with stem and subparallel to posterior leaf-margin, usually forming an obliquely ovate sac (Pl. 14, figs. 1-2, 7); perianth terete, 5-10 angled, erect; yellow green plants 15

15. Minute plants with distant leaves, less than 0.5 mm wide and 1 cm long (Pl. 14, fig. 2); ventral lobes 1/2 - 2/3 the dorsal in size (Pl. 14, fig. 1) ..... *Microlejeunea*

15. Moderate sized plants, with approximate to subimbricate leaves; over 0.5 mm wide and mostly 0.8-1.5 cm long; ventral lobes less than 1/4 the dorsal in size (Pl. 14, fig. 7) ..... *Lejeunea*

6. Leaves never sharply complicate-bilobed (Pls. 3-11), never with a small ventral "lobule" (in a few species 2-lobed, with the lobes loosely lying over each other, but not separated from each other by a keel) 16

16. Leaves incubous (the dorsal leaf margin lying over the posterior, ventral margin of the leaf directly *anterior* to it) (Pl. 2, figs. 2, 5, 8); underleaves large and distinct throughout (Pl. 2, figs. 3-4, 7, 10-13); rhizoids of leafy shoots present only at base of underleaves, in a definite rhizoid-initial area (Pl. 2, figs. 7, 10, r) 17

17. Leaves about 1/2 divided into 3-4 lobes (Pl. 2, fig. 5); flagellae common; underleaves similarly 3-4-lobed as leaves ..... *Lepidozia*

17. Leaves merely 2-3-toothed at apex, or entire (Pl. 2, figs. 2, 6, 12); underleaves crenate-dentate, or merely bilobed (Pl. 2, figs. 3, 7, 13) 18

18. Hyaline, pale to bluish-green; leaves entire or obsoletely bidentate at tips (Pl. 2, figs. 6-8, 11-13); flagelliform branches with minute leaves absent; gemmae often present on erect filiform shoots; rhizoids many from well-developed initial regions at base of underleaves (Pl. 2, fig. 7, r) ..... *Calypogeia*

18. Opaque, yellow to bright green to reddish-brown; leaves always with some at least tridenticulate at apex (Pl. 2, figs. 2-4); flagelliform shoots common (Pl. 2, figs. 2, 4); gemmae absent; rhizoids few or very few at bases of underleaves, scarcely forming a distinct area ..... *Bazzania*

16. Leaves succubous (Pl. 7, fig. 1; Pl. 8, fig. 7; Pl. 10, figs. 1, 6) (the dorsal leaf margin lying over the anterior, ventral margin of the leaf directly *behind* it) or transversely inserted (Pl. 4, figs. 1, 12; Pl. 9, figs. 6, 8; Pl. 11, fig. 5) 19

19. Leaves prominently 2-4 lobed on *all* leaves (Pl. 4, figs. 1, 11, etc.) 20

20. Leaf-insertion narrow and constricted (less than 1/4 the maximum width of leaf); leaves bilobed, with the ventral margin incurved to form a sac, the filiform lobes running out in a cilium 5-7 cells long and one cell wide; only on rotting wood ..... *Nowellia*

20. Leaf-insertion over 1/4 the maximum width of leaf, not constricted (Pl. 4, fig. 11; Pl. 8, figs. 3, 9; Pl. 3, figs. 2, 11); leaf-apices not running out in long cilia 21

21. Leaves transversely inserted (Pl. 4, fig. 12; Pl. 9, figs. 6, 8; Pl. 11, fig. 5) (the lobes sometimes conduplicate); perianth 4-many plicate, terminal, or absent 22

22. Leaves more than twice as wide as stem, 2-5 lobed (Pl. 7, fig. 16; Pl. 11, fig. 5), each lobe more than 8 cells wide at base;

underleaves quite absent; cells large, usually mostly over 18 μ long in leaf-middle; plants not filiform in appearance (except for occasional erect, gemmiparous shoots) 23

23. Perianth well-developed (Pl. 7, fig. 16), more or less plicate and contracted to mouth, free from bracts; leaves 2-5 lobed, the sinuses usually descending 1/4 the leaf-length or more (Pl. 7, fig. 14; Pl. 9, figs. 6, 8-9); never aquatic or subaquatic; 1-2 celled gemmae usually present (Pl. 7, fig. 15; Pl. 9, figs. 5, 7) ..... *Lophozia*, s. lat.

23. Perianth obsolete, shorter than bracts and fused with them for nearly its entire length (Pl. 11, fig. 6, c); leaves bilobed 1/10 - 1/3, the lobes often obtuse or rounded (Pl. 11, fig. 7); gemmae lacking ..... *Marsupella*

22. Leaves little wider than the filiform stem, very distant to nearly approximate, 2-lobed 1/2 - 3/4, each lobe 2-6 (8) cells wide at base (Pl. 4, figs. 11-12; Pl. 5, fig. 5; Pl. 6, figs. 4, 8); underleaves frequently distinct; cells small, 10-16 (rarely 25 μ); plants quite filiform (Pl. 4, fig. 7) ..... *Cephaloziella*

21. Leaves distinctly succubously inserted (the lobes never conduplicate) (Pl. 3, fig. 7; Pl. 7, fig. 1; Pl. 10, fig. 9-12); plants never minute and filiform 24

24. Underleaves large, conspicuous (Pl. 10, figs. 10-12), either deeply bilobed or lanceolate and entire, with or without a lateral marginal tooth; perianth absent, on short postical shoots, or trigonous (with third keel dorsal); leaves never 3-4-lobed; cells thin-walled, with no or small trigones 25

25. Underleaves bilobed, each lobe bearing a lateral slender tooth (Pl. 10, figs. 10-11); rhizoids strictly limited to the base of the underleaves; perianth trigonous and terminal; male shoots on normal (not ventral) shoots ..... *Lophocolea*

25. Underleaves entire and lanceolate or simply bifid (Pl. 10, fig. 12), never with lateral cilia or teeth; rhizoids not strictly limited to base of underleaves; perianth or perigynium present: always from short ventral branches and appearing on the side of the main axis; male inflorescences reduced ventral shoots (Pl. 10, fig. 12) 26

26. Underleaves entire and lanceolate or ovate, often connate at base with the base of a lateral leaf; perianth present; leaf-sinus usually broad and lunate; plants not opaque in appearance ..... *Harpanthus*

26. Underleaves simply bifid to base (Pl. 10, fig. 12), free from the leaves; perianth absent, but a rhizoidous, subterranean perigynium present; leaf-sinus usually sharp to rectangular, deep (Pl. 10, fig. 12); plants very opaque ..... *Geocalyx*

24. Underleaves absent or minute, if present usually of only 1-6 cells;[6] rhizoids scattered all over the ventral side of the stem, but often very few (Pl. 9, fig. 11; Pl. 8, fig. 17); leaves 2-5-lobed; androecia never small, spike-like ventral shoots 27

27. Leaves with two obtuse, rounded lobes (Pl. 9, figs. 11, 13-

[6] In one species (*Lophozia rutheana*) with large, many-ciliate underleaves. This species has knot-like bulging trigones.

14); lower leaves quite or very distant; cells thin-walled or equally thickened; plants often blackish-green or fuscous-green; oil-bodies present; gemmae lacking 28

28. Flagellae absent; branches all or nearly all lateral; perianth caducous, inflated smooth, terminal on main shoot; not in peat bogs; leaves ovate-orbicular (Pl. 9, figs. 11, 13-14) ..... *Gymnocolea*

28. Flagellae present; branches all occurring ventrally; perianth from short ventral branches, trigonous, non-caducous; in peat bogs only; leaves oblong-rectangular ..... *Cladopodiella*

27. Leaves acutely 2-5 lobed (Pl. 7, figs. 2, 7, 11, 14); leaves usually approximate to subimbricate; plants rarely blackish or fuscous green; 1-2 celled gemmae often present (Pl. 7, fig. 15; Pl. 8, fig. 8) 29

29. Stem with the cortical, outer layer of cells large, pellucid (much larger than the interior cells, which can be seen by transmitted light as an opaque strand of small cells) (Pl. 3, figs. 2, 7); leaves roundish or oval, bi-lobed, the sinus often lunate, the lobes often connivent (Pl. 3, figs. 2, 7, 9, 11); cells thin-walled or equally thick-walled, pellucid, nearly or quite lacking oil-bodies; perianth on short ventral branches, trigones (Pl. 3, figs. 4, 8) ..... *Cephalozia*

29. Stem with outer layer of cells smaller than or equal in size to inner cells, opaque, often thick-walled; leaves 2-5 lobed, the lobes never connivent (Pls. 7-9); cells mostly with distinct trigones (Pl. 7, figs. 12-13; Pl. 8, figs. 1, 6), rarely pellucid, always with distinct oil-bodies; perianth terete, plicate or smooth above, never trigonous (Pl. 7, fig. 1; Pl. 8, figs. 2, 17) ..... *Lophozia*, s. lat.

19. Leaves entire (Pl. 10, figs. 1, 6, 7; Pl. 11, figs. 1, 9) (rarely a few retuse or emarginate, especially on immature shoots; in one species margin often finely denticulate) 30*

30. Yellow-green exogenous gemmae occurring in abundance (either at apices of lanceolate leaves, or at apices of erect, slender shoots) (Pl. 11, figs. 1, 2); cells with very large, bulging trigones (Pl. 11, figs. 3-4); lower leaves, at least, circular or nearly (Pl. 11, fig. 1); small underleaves present 31

31. Upper, gemmiparous leaves large, spreading ovate-lanceolate or lanceolate (Pl. 11, fig. 1); leaf-cells over 45 μ long; flagellae absent; in peat bogs; perianth laterally compressed, terminal ..... *Mylia*

31. Upper, gemmiparous leaves small, appressed to the erect, filiform shoots: leaf-cells under 30 μ; flagellae present; on decaying logs; perianth trigonous, on short ventral shoots ..... *Odontoschisma*

30. Gemmae absent (in one species endogenously produced in apices of swollen stems); cells with trigones minute or absent[7]; flagellae absent; leaves never lanceolate and cells under 40 μ 32

32. Large underleaves present throughout, bifid with a tooth on each lobe, visible at 20 x (Pl. 10, fig. 5); perianth from short lateral branch; the perianth short, scarcely or not longer than calyptra

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[7] In *Jungermannia lanceolata* with large trigones in the rectangular leaves.

* See also supplementary key in Appendix, following p. 703.

(Pl. 10, fig. 6); rhizoids from distinct area (Pl. 10, fig. 5) at base of underleaves; leaves elongate, rectangular ..... *Chiloscyphus*

32. Underleaves small or absent, entire; perianth terminal on main shoot (Pl. 10, fig. 7; Pl. 11, fig. 9), much longer than calyptra; rhizoids all along stem, or virtually none 33

33. Posterior (dorsal) leaf-margin distinctly reflexed[8]; leaves decurrent both on ventral and dorsal bases, with the ventral margins usually at least slightly denticulate; perianth laterally compressed; rhizoids virtually absent, except on the basal rhizomatous stems .....*Plagiochila*

33. Posterior leaf-margin not reflexed; leaves not or scarcely decurrent either dorsally or ventrally (Pl. 10, figs. 1, 7), with the margins never denticulate; perianth terete, not compressed (Pl. 10, figs. 4, 7; Pl. 11, fig. 9); rhizoids abundant, no rhizomatous basal, creeping stems 34

34. Female bracts quite entire (Pl. 10, fig. 7; Pl. 11, fig. 9); perianth merely crenulate at mouth (Pl. 10, fig. 7; Pl. 11, fig. 9); underleaves quite lacking; leaves circular, ovate or cordate (if oblong-rectangular with bulging trigones); perianth beaked or not; bracteole absent 35

35. Leaves circular (either margined with a row of large, swollen cells (Pl. 10, figs. 7, 8), or the rhizoids violet); perianth more or less fused with and clasped by bracts at base; gemmae absent .....*Plectocolea*

35. Leaves various (if circular the stem-apices are swollen and internally gemmiparous), never margined; rhizoids not violet; perianth entirely free from bracts .....*Jungermannia*

34. Female bracts ciliate at least at dorsal base (Pl. 10, figs. 2, 4); perianth ciliate at mouth, not beaked (Pl. 10, figs. 3, 4); small underleaves distinct (at least on fertile plants); bracteole large, ciliate (Pl. 10, fig. 2); leaves ovate- or oblong rectangular, longer than wide (Pl. 10, fig. 1), occasionally some retuse or bilobed .....*Jamesoniella*

Family PTILIDIACEAE

I. PTILIDIUM Nees

KEY TO SPECIES

1. Cilia of leaf margins distinctly longer than basal width of leaf-lobes (Pl. 1, figs. 2, 7); dorsal leaf-lobe merely 6-12 cells wide at base; leaf-sinuses descending 2/3 - 3/4 the leaf length .....*P. pulcherrimum*

1. Cilia of leaf margins not or scarcely longer than basal width of dorsal leaf-lobe (Pl. 1, figs. 4-5); the latter at least 15-20 cells wide at base; leaf-sinuses descending 1/2 - 2/3 the leaf-length .....*P. ciliare*

P. CILIARE (L.) Hampe

Rare and extremely local in our region. TOMPKINS CO.: Sixmile Creek Ravine, below Potter's Falls, *R. M. & O. M. Schuster*. ONTARIO CO.: Briggs Gully, Richmond, near Honeoye Lake, *Schuster*. CHEMUNG CO.: Elmira (*Barbour 888, 1900*); reported by Frye and Clark (1943), but not seen by writer.[9] (Also reported from Western New

8 Especially in drying.

9 Probably misidentified, since all of the numerous Barbour specimens from the New York-Pennsylvania area examined prove to be *pulcherrimum*.

York by Day 1882, p. 166, and from Onondaga County by Goodrich 1912, p. 24, but these records are almost certainly the more common *P. pulcherrimum*, and should not be accepted without study of the actual specimens).

The present species is decidedly more northern in distribution than the next, which almost entirely replaces it in the Transition Zone, i.e., in the area of the Beech-Maple-Hemlock-Yellow Birch Climax. Although further northward the species is quite ubiquitous and occurs on subcalcareous as well as decidely acidic ledges and rocks, it becomes extremely restricted in distribution near its southern limits. Confusion with *P. pulcherrimum* in all of the older literature leaves the actual southern limits of the distribution of the species in doubt, but the present records are certainly from the very periphery of its range. Locally it has been found on moist, shaded humus, beneath Hemlock, on a cold, depressed, swampy slope (Tompkins Co.), and on the exposed, north-facing crest of a ravine, on thin soil over non-calcareous shale (Ontario Co.). The difference in distribution between the two species of the genus would indicate that they might better be treated as subspecifically distinct, were it not for the fact that they occur together in both the Transition and Canadian Zones, yet remain perfectly distinct.

This species and *P. pulcherrimum* can be separated from all our other Hepaticae because of the possession of many slender, long cilia at the margins of the several-lobed leaves and underleaves (Pl. 1, figs. 4-7). *Trichocolea* shares these characteristics, but differs in lacking trigones of the leaf-cells (Pl. 1, fig. 9), lacking a perianth, and in having the leaf-lamina much more strongly reduced, and scarcely evident (Pl. 1, fig. 8); it is furthermore a larger species, pale yellowish-green, never reddish or brownish-tinged, and is very regularly bipinnately branched.

The much looser growth (Pl. 1, fig. 4), more erect habit, and tendency to form deep, loose tufts distinguish this species from *P. pulcherrimum*. A hand-lens will reveal the presence of a much wider lamina (often 20-25 cells wide) and sparser, shorter marginal cilia (Pl. 1, fig. 5) in this species, contrasted to *P. pulcherrimum*, which has the lamina of the leaf only to 10-12 cells wide near the base of the dorsal lobe, and has the cilia slender, numerous, more elongate; *pulcherrimum* furthermore has the leaves more imbricate, and grows closely applied to the substratum, in much more shallow mats (Pl. 1, fig. 2).

P. PULCHERRIMUM (Web.) Hampe

Abundant and widespread. TOMPKINS CO.: Slaterville Springs; McLean Bogs; Sixmile Creek; Buttermilk Glen; Fall Creek; Old Buttermilk Glen; Enfield Ravine; Coy Glen; Ellis Hollow Swamp; McKinney's Twin Glens; Taughannock Ravine; Lick Brook; Cascadilla Ravine; Woodwardia Swamp; Freeville Fir Tree Swamp; Renwick Brook; swamp near source of Sixmile Creek; Varna; Headwaters Swamp; Michigan Hollow Swamp; South Hill Marsh; Esty Glen; Pony Hollow, Newfield; Key Hill, Newfield. CORTLAND CO.: Homer Gulf, Homer; Virgil; east of Solon. ONONDAGA CO.: "Tamerac Swamp') (Goodrich 1912, p. 24, as *P. ciliare*); Clark Reservation near Jamesville; "Onondaga Co." (Underwood and Cook, Hep. Amer. No. 11). CHEMUNG CO.: Veteran; swamp 1 mile from southwest corner of county. TIOGA CO.: Richford; east of Caroline; swamp near North Spencer; Headwaters Swamp. SENECA CO.: Junius Sphagnum Bogs. SCHUYLER CO.: Watkins Glen. ONTARIO CO.: Canandaigua; Briggs Gully, Rich-

mond; Farmington. MADISON Co.: Chittenango Falls. MONROE Co.: Irondequoit Bay. GENESEE Co.: Bergen Swamp. STEUBEN Co.: Woodhull. ALLEGANY Co.: Alma. CATTARAUGUS Co.: near Rock City; Alleghany State Park; Swamp near Crystal Lake, with *Jamesoniella*. CAYUGA Co.: Paines Creek near Aurora. CHENANGO Co.: Plymouth Pond, S. Plymouth; Peat Bog near S. Plymouth.

This species and *Nowellia curvifolia*, together with *Lophocolea heterophylla*, are among the dominant members of the *Nowellia-Jamesoniella* Associule occurring on rotting, rather shaded to exposed, moderately moist decorticated logs of the deciduous woods of the Transition Zone. Although the species occurs commonly on cliffs and ledges away from central and western New York, it does so in this area only rarely (Sixmile Creek, and Briggs Gully). The reason appears to be local lack of tolerance of the species for a calcareous substratum. It is common, however, in the limited quartz-conglomerate area near Rock City, occurring on moist rocks with such Canadian species as *A. minutus*, *A. michauxii*, and *Bazzania denudata*. Locally, therefore, the species appears to be "calciphobous." On the leached soil of the ravine-tops, where the soil is acid by virtue of the washing-out of any lime originally present, and by the formation of humus by the needles of hemlock and the leaves of oak, the species occurs rather abundantly, often associated with *Jamesoniella autumnalis* and *Lophozia barbata* (Briggs Gully, Sixmile Creek, and Fall Creek). The species occurs often around the butts of living trees, and frequently invades the surrounding soil; very rarely it invades the bark farther up (4-6 feet above the ground), as in Headwaters Swamp, where it grew associated with *Frullania eboracensis*, *F. asagrayana* and a depauperate form of *Bazzania trilobata*.

For differentiation, see *P. ciliare*.

II. TRICHOCOLEA Dumort.

T. TOMENTELLA (Erh.) Dumort.

Frequent: TOMPKINS Co.: McLean Bogs; Coy Glen; Sixmile Creek; Sixhundred Ravine; Michigan Hollow Swamp; West Danby; Enfield Glen; Lick Brook; Key Hill in Newfield; Headwaters Swamp; Ellis Hollow Swamp; marsh west of Newfield; Ringwood Swamp. CORTLAND Co.: Green Lake, Preble; Homer Gulf, Homer; Kenney Brook Gulf. Truxton. GENESEE Co.: Bergen Swamp (Day 1882, p. 166). CATTARAUGUS Co.: "in most of the swamps and bogs of the county" (Boehner 1943, p. 11.) TIOGA Co.: southern part of Headwaters Swamp. MADISON Co.: Chittenango. ONONDAGA Co.: White Lake, Jamesville; "Tamerac Swamp" (Goodrich 1912, p. 24); Onondaga Co. (Underwood and Cook, Hep. Amer. No. 13). WAYNE Co.: Arbor-Vitae Swamp east of Clyde. ONTARIO Co.: Briggs Gully, Richmond.

This species is most abundant on rotting logs and stumps that have turned into humus, lying in shallow water in swamps, and on moist muck in such situations, often forming *marsen-vegetation*, together with *Cephalozia connivens*, *media*, and *Geocalyx*; it is limited to densely shaded areas in such swamps. Under shaded conditions on moist-to-wet shale and sandstone ledges, or on thin soil over such ledges, consistently on the north-facing sides of ravines, it occasionally is an abundant species, associated here with *Moerkia*, *Geocalyx graveolans*, etc. It may occur both on non-calcareous and calcareous ledges, indicating it has a moderate toleration for lime; this is indicated

especially by the fact that it occurs almost always in places where *Moerkia* is found, a genus whose distribution is influenced by the presence of at least traces of lime in the substratum. The species thus has a wide toleration as far as the nature of the substratum is concerned; the main requirements appear to be an abundant, constant supply of moisture and relatively diffuse light.

Reproducing material is very rarely found (Coy Glen, *Andrews,* 1918; Sixmile Creek, *Schuster,* 1945; Briggs Gully, *Schuster,* 1945); the calyptras mature in autumn, the green capsules frequently bursting through the fleshy calyptra by late October; in early spring, the last of April through late May, the setae elongate and spores are distributed.

The very pale-green color, very large size, regularly bipinnatified appearance, and dissolution of the lamina into cilia are characteristic (Pl. 1, figs. 8-10).

III. BLEPHAROSTOMA Dumort.

B. TRICHOPHYLLUM (L.) Dumort.

Infrequent locally, often overlooked. TOMPKINS CO.: Ringwood Swamp, *R. M. & O. M. Schuster,* 1943; Coy Glen, *sev. coll.;* Enfield Glen, *sev. coll.;* Cascadilla Glen, *Wiegand;* Sixmile Creek Ravine, *R. M. & O. M. Schuster,* 1943; Sixhundred Ravine, *R. M. & O. M. Schuster;* Ontario Briggs Gully, Richmond, *Schuster.* CORTLAND CO.: Homer Gulf, Homer, *Wiegand;* Kenney Creek Gulf, Truxton, *Wiegand.* MADISON CO.: Chittenango Falls, *R. M. & O. M. Schuster.* GENESEE CO.: Bergen Swamp, *R. M. & O. M. Schuster.* ONONDAGA CO.: Jamesville (Underwood & Cook, Hep. Amer. No. 33); Onondaga Valley (Goodrich 1912, p. 22). CATTARAUGUS CO.: north of Rock City, *Schuster & Rader;* Jones Hill, Steamburg (Boehner 1943, p. 11). CHENANGO CO.: Plymouth Pond, S. Plymouth, *Schuster & Winne* (with *C. trichomanis*).

Occurring locally on somewhat sandy to loamy, moist, shaded slopes and banks, on circumneutral to acid soils; more occasionally on rotting wood and humus as a member of the *Nowellia-Jamesoniella* Associule; very rarely on moist vertical rocks. The most commonly associated species are *Lepidozia reptans, Bazzania trilobata, Jungermannia lanceolata, Cephalozia media, Calypogeia trichomanis,* and *C. neesiana.* Locally, it occurs in combination in three distinct associules: one with *Calypogeia* and *Cephalozia* on shaded, moist, loamy or sandy-loamy banks; a second on humus and very decayed wood, with *Lepidozia* and *Bazzania,* as well as *Jungermannia lanceolata* and *C. trichomanis,* and a locally rare associule of vertical, moist ledges and cliffs, associated with *Lepidozia,* rarely with *Bazzania denudata, "Lophozia" minuta, A. michauxii,* and *T. exsecta.* The latter associule is rare in our region possibly because of the scarcity of acidic rocks; I have found it but twice, on non-calcareous sandstone in Sixhundred Ravine, and on moist quartz-conglomerate ledges near Rock City. In the Coniferous Panclimax the species appears to be most at home on such moist, shaded cliffs and ledges, however, most often growing near the bottom of vertical rocks, where capillary action can keep a whole mat moist by drawing water from the ground.

The small size, bright green color, and the transverse, 4-parted leaves separate this species from all others, except only the two species of *Microlepidozia*; the more elongate, more filiform leaf-segments, wide one cell to base, and the terminal position of the perianth at once separate *Blepharostoma* from *Microlepidozia* (Pl. 1, fig. 1).

Family LEPIDOZIACEAE

I. BAZZANIA S. F. Gray

KEY TO SPECIES

1. Plant strongly brownish pigmented, with decidedly deflexed leaves with acute apices bearing 1-3 small teeth; caducous leaves absent; 1.3-2.0 mm wide ..... *B. tricrenata*

1. Plant pale or yellow green to deep green, never brownish; leaves not or scarcely deflexed 2

2. Caducous leaves present (portions of the stem thus often largely denuded of leaves); small, pale yellowish-green to green plants less than 1.8 mm wide ..... *B. denudata*

2. Caducous leaves absent (Pl. 2, figs. 2-4); large, usually deep green species with shoots 3-6 mm wide ..... *B. trilobata*

B. TRICRENATA (Wahl.) Trevis

Very rare locally, confined to the unglaciated region (and its periphery), from 2000 feet upwards. CATTARAUGUS CO.: Martiny Rocks, West Branch of the Four Mile Road, Allegany (Boehner 1943, p. 11).

This species is usually strictly montane in distribution, even more strictly so than *B. denudata.* Boehner (*loc. cit.*) states that it is "a rather common species in our range" but gives only the single station cited above. The almost entirely saxicolous occurrence, together with a generally distinct "avoidance" of calcareous rocks, would eliminate it from most of central and western New York, even were the elevation sufficient. The species very probably does not occur below the zone of 90-120 frost-free days. Commonly associated are other members of the *Lophozia-Scapania* Associule of vertical, moist shaded, north or northwest-facing cliffs, such as *A. (Sphenolobus) minutus, Anastrophyllum michauxii, Scapania nemorosa,* rarely *S. subalpina, L. (Orthocaulis) gracilis, Bazzania trilobata* and *denudata,* and the more widespread *Tritomaria exsecta* and *exsectiformis,* as well as *Blepharostoma trichophyllum, Lepidozia reptans* and *Ptilidium.* Various lociations of this associule are extremely widespread and very rich in species, especially in the Coniferous Panclimax. Locally the associule occurs as a much attenuated peripheral society, with all or most of the species secondary invaders or chasmophytic in nature.

The brownish pigmentation of the whole plant, the rather acute leaf-apices and narrow form of the leaf, and absence of caducous leaves separates the species from *B. denudata,* with which it was at one time much confused. The much smaller size, as well as above characters separate it from *B. trilobata.*

B. DENUDATA (Torr.) Trevis

Rare and very local in our region. CATTARAUGUS CO.: About one mile north of Olean Rock City, *Schuster & Rader;* Olean Rock City (Boehner 1943, p. 11); Martiny Rocks, West Branch of the Four Mile Road, Allegany (Boehner 1943, p. 11).

Together with the above species occurring under more montane and colder conditions than the common lowland species, *B. trilobata.* Most widespread as a member of the *Lophozia-Scapania* Associule of north or northwest

facing, moist vertical ledges and cliffs together with the above species and under similar conditions, but elsewhere becoming corticolous — the calcium tolerance not accurately known but apparently low. Restricted in our area to the same unglaciated area as is the above species and apparently a glacial relic of disjunct distribution in the Appalachians. Almost certainly occurring in northern Pennsylvania, since the present stations come within 2-3 miles of the borders of that state; not yet reported from there.

Similar, superficially, to a small form of *B. trilobata* (with which it may grow on moist cliffs), but differing at once in the caducous leaves and much smaller size.

B. TRILOBATA (L.) Gray

Common, rather widespread. TOMPKINS CO.: Coy Glen; Lick Brook; Enfield Glen; Old Buttermilk Ravine; Cascadilla Glen; Buttermilk Ravine; Fall Creek; McLean Bogs; Sixmile Creek Ravine; Sixhundred Ravine; Headwaters Swamp; Michigan Hollow Swamp; Key Hill in Newfield; Woodwardia Bog; Malloryville Bog; Freeville Bog; Fir Tree Swamp near Freeville; three miles south of Dryden; Ringwood Swamp; West Danby. ONONDAGA CO.: White Lake, Dewitt; Jamesville Road (Goodrich 1912, p. 22); "Onondaga Co." (Underwood & Cook, Hep. Amer. No. 12). CATTARAUGUS CO.: north of Rock City; Waterman Swamp; Martiny Rocks. HAMILTON CO.: Mud Pond. MADISON CO.: Cazenovia; Chittenango Falls. TIOGA CO.: southern part of Headwaters Swamp. CORTLAND CO.: Beaver Brook, South Cortland; near E. Freetown; Robbins Glen, Truxton. GENESEE CO.: Bergen *Swamp*. ONTARIO CO.: Briggs Gully, Richmond. CHENANCO CO.: Plymouth Pond, S. Plymouth.

This is one of our dominant species of the shaded, moist, sheltered woods, and shaded swamps, of the Transition Zone; it abounds especially on the moist, shaded, protected slopes of the ravines, forming part of the Hemlock-Yellow Birch Subclimax. It is also abundant, and particularly luxurious, in the Pine-Hemlock—Yellow Birch Swamp and Bog Subclimax, where it may form deep, soft dark green mats of considerable extent, carpeting old Hemlock logs and stumps (i.e., under decidedly acid conditions); it occurs here thus on elevated points, often somewhat higher than the low, more decidedly hygric niches invaded by *P. asplenioides* and *T. tomentella*. The large, caespitose, crowded mats represent an advanced phase, successionally: the species obviously always following lociations of the *Nowellia-Jamesoniella* Associule (usually the more shade-loving *Riccardia latifrons-Cephalozia* lociation). Commonly associated are *Plagiochila asplenioides, Lepidozia reptans,* but especially *Dicranum*. More rarely the species occurs on moist, humus covered, decaying-logs, with *Geocalyx, Cephalozia, Lophozia,* etc.; very rarely (Ringwood) it may invade *Sphagnum* at the edges of swamps. The relatively low precipitation and humidity of our region prohibits its growth on tree-trunks, except very rarely, as at Lick Brook and Headwaters Swamp (there occurring as a depauperate modification, with somewhat caducous leaves, close to the forma *depauperata* of Müller.) The species is a decided calciphobe, and does not occur on moist rocks to any extent (except occasionally on the acid quartz-conglomerate near Rock City); local distribution indicates the species can tolerate lime in minute amounts, however. A decided humicole and normally meso-hygrophytic.

The large size, generally deep green color, large, irregularly dentate

amphigastria, and shortly 3-lobed leaves (that are never caducous) at once distinguish this species; the incubous leaves separate it from all but several closely related forms. (Pl. 2, figs. 2-4)

II. LEPIDOZIA Dumort.

L. REPTANS (L.) Dumort.

Infrequent locally: TOMPKINS CO.: Sixmile Creek Ravine, *R. M. & O. M. Schuster;* Woodwardia Bog, *R. M. & O. M. Schuster;* Fir Tree Swamp near Freeville, *Schuster & Rader;* Coy Glen, *sev. coll.;* Enfield Glen, *sev. coll.;* Cascadilla Glen, *Wiegand,* 1893; Sixhundred Ravine, *R. M. & O. M. Schuster.* CORTLAND CO.: Mud Hole, Beaver Brook; e. of Solon, *Schuster & Winne;* Beaver Brook near South Cortland, *Andrews, Schuster.* MADISON CO.: *Chittenango.* ONTARIO CO.: Briggs Gully, Richmond, *Schuster.* ONONDAGA CO.: Jamesville Road (Goodrich 1912, p. 23); Jamesville (Underwood & Cook, Hep. Amer. No. 14). CATTARAUGUS CO.: north of Rock City, *Schuster & Rader;* Martiny Rocks, Allegany. (Boehner 1943, p. 11). GENESEE CO.: Bergen Swamp, *R. M. & O. M. Schuster.* CHENANGO CO.: Bog near S. Plymouth, *Schuster & Winne.*

A pronounced humicole, like *Bazzania trilobata,* and frequently occurring with it. Unlike that species it commonly occurs also on moist, shaded, sheltered rocks, especially on their vertical faces. Its local rarity on rocks appears in part to be due to the low toleration for lime this species exhibits (at least in the southern portion of its range). Further northward the species exhibits a wide toleration for differences in calcium concentration and pH. I have found it once in Sixhundred Ravine, on moist sandstone associated with *Blepharostoma,* and a second time, on wet quartz-conglomerate ledges, at Rock City, with such "Canadian" species as *Bazzania denudata, Anastrophyllum michauxii, A. minutus,* etc. as well as with the *Blepharostoma,* as a member of the *Lophozia-Scapania Associule.* It occurs also more frequently on very rotten wood than *B. trilobata.* The two most essential requirements of the species appear to be a constant, moderate supply of moisture and a lack of direct sunlight, therefore it is almost entirely a species of densely forested regions and of the ravine-slopes.

The generally strongly deflexed, 4-lobed, hand-like leaves (Pl. 1, fig. 5), the yellow-green to green color, the regularly bipinnate appearance, and the decidedly incubous leaves are characteristic. The smaller size as compared with *Bazzania,* and superior size to that of *Microlepidozia,* at once separates it from all related forms.

III. MICROLEPIDOZIA (Spr.) Joerg.

KEY TO SPECIES

1. Underleaves with 1-2 of the lobes regularly aborted, reduced in length; female bracts and perianth-mouth with very short cilia; on sandy soil ..... *L. sylvatica*
1. Underleaves with all 3-4 divisions regularly developed, similar in length (Pl. 1, fig. 1, u); bracts and perianth-mouth with long cilia, deeply laciniate; in bogs ..... *L. setacea*

M. SETACEA (Web.) Joerg.

Very rare and local: GENESEE CO.: on rotting, wet log in Bergen Swamp, 1945, *R. M. & O. M. Schuster;* among *Sphagnum,* Bergen Swamp, 1907, *E. J. Hill;* 1946, *Schuster & Winne.*

This species appears to be very local and rare. I have been unable to discover it in any of our other *Sphagnum* bogs. The occurrence on rotting wood, noted above, is somewhat unusual, the species occurring nearly invariably among *Sphagnum*.

Goodrich (1912, p. 23) reports this species from Onondaga County. The reference should perhaps be transferred to *L. sylvatica*, which is a much commoner species, throughout most of its range.

Commonly associated with *M. setacea* are *Mylia anomala, Cephaloziella, subdentata* and *elachista, Cladopodiella fluitans*, and other species of the *Mylia* Associule. When present on wet, rotting logs, *Calypogeia neesiana, Cephalozia connivens, Lophozia porphyroleuca* and *L. incisa* frequently occur with it. E. J. Hill who first reported the species from our area gave a discussion of the nature and function of the swollen rhizoids (Pl. 2, fig. 1, r) of this species that needs correction. He considered that the rhizoids functioned as hold-fasts and as supports for the species. Such is not the case, for Müller (1905-1916, p. 289-291) demonstrated that the swollen tips of the rhizoids contained fungal hyphae, and that some sort of symbiotic relationship existed between the fungus and the hepatic, whereby the hepatic was provided with nitrogen. It may be interesting to point out that my material which grew on a rotten log in the swamp, was not provided to any noticeable degree with swollen rhizoids. There appears to be a correlation between occurrence on a nitrogen-poor substrate and presence of mycorhizal infection, and occurrence on a moderately nitrogen-containing substrate, and absence of these fungal hyphae.

M. setacea differs from *sylvatica* in a number of regards: it does not have one or more of the lobes of the amphigastria suppressed, but has them all equally developed; the perichaetial bracts are deeply laciniate, similarly to the perianth mouth (in *sylvatica* short-ciliate, with the cilia 1-3 cells long). The present species occurs almost constantly on *Sphagnum*, rarely on decaying logs at the fringes of bogs; *L. sylvatica*, on the other hand occurs chiefly on sandy soil or thin soil on ledges, chiefly of acidic rocks, often with *Cephalozia* and *Bazzania*.

Both forms may be mistaken for both *Cephaloziella* and *Blepharostoma*, since the facies and color are largely similar, as well as the size. The bilobed leaves of *Cephaloziella*, with each lobe at least 3-4 cells wide basally, and with the under-leaves less well-developed than the leaves, separates the latter; the more filiform leaf-lobes of *Blepharostoma*, with each lobe only a single cell wide, separates that genus.

(M. SYLVATICA (Evans) Joerg.

Very doubtfully present: ONONDAGA CO.: Marcellus (Goodrich 1912, p. 23, as *L. setacea*).

I think the Goodrich citation should tentatively be placed under *M. sylvatica*, since *setacea* is much more rare in America, and is confined to *Sphagnum* bogs and their fringes, as far as known. (At the time of the above citation (1912) the two species were not generally distinguished.)

Family CALYPOGEIACEAE

I. CALYPOGEIA Raddi

KEY TO SPECIES

1. Amphigastria divided 2/3 - 3/4 their length, 1-2 times as wide as stem on well-developed, mature stems; lobes of amphigastria acute or obtusely angulate, never broadly rounded (Pl. 2, figs. 10-12, 14); marginal cells of leaf apices 1.0-1.3 as long on margins as wide 2

2. Cells in leaf-middle 32-35 x 36-40 μ, the marginal apical cells only 24-31 μ; amphigastria scarcely to little wider than stem, as long or longer than wide, with subacute lobes (Pl. 2, figs. 10-11); cells often with trigones or thick-walled; in bogs only; plants less than 1.8 mm wide; oil-bodies to 5-7μ long, colorless ..... *C. sphagnicola*

2. Cells in leaf-middle 35-40 x 40-80 μ, the marginal apical cells mostly 32-40 μ; cells always thin-walled and lacking trigones; plants usually larger 1.8-3 mm wide; oil-bodies to 12-14 μ long 3

3. Oil-bodies colorless; lateral leaves ovate and usually longer than wide (Pl. 2, fig. 12), at apex pointed or slightly bidentate; underleaves much wider than stem, wider than long, the lateral margins usually armed with an obtuse tooth (Pl. 2, fig. 12) ..... *C. fissa*

3. Oil-bodies bluish; lateral leaves broader than long (Pl. 2, fig. 12), obtusely pointed or rounded at apex; underleaves little or scarcely wider than stem, about as long as wide, the lateral margins unarmed (Pl. 2, fig. 14) ..... *C. trichomanis*

1. Amphigastria divided 1/3 - 0 their length, on well-developed shoots 2-3.5 as wide as stem, wider than long, the lateral margins not or occasionally obtusely armed; lobes, if present, very broadly rounded (Pl. 2, figs. 7, 9, 19); marginal cells of leaf-apices sometimes elongate; oil-bodies colorless 4

4. Underleaves shortly bilobed (occasionally divided 1/3 - 2/5), the lobes broadly rounded; cells of underleaf-middle 25 x 46-60 μ or larger; leaves broadly ovate, narrowed at base usually, about as wide as long (Pl. 2, figs. 6-9), with cells in leaf-middle 38-40 x 48-76 μ or even larger; spores 14-16 μ; oil-bodies in all leaf and underleaf cells ..... *C. mülleriana*

4. Underleaves entire or merely retuse-emarginate (Pl. 2, fig. 13), never bilobed, the cells in the middle 15-18 x 33-40 μ, rarely somewhat larger; leaves obliquely elliptical to ovate, distinctly longer than wide (Pl. 2, fig. 13), with cells of the leaf-middle usually 32-36 x 38-44 μ; oil-bodies absent in all or most underleaf cells; spores 10-12 μ 5

5. Leaf-apices evenly, narrowly rounded, not margined by cells that are elongate parallel to the margin; leaf-shape obliquely ovate, widest near base; rhizoid-initial region at base of underleaves ovate, less than twice as wide as high; oil-bodies in all cells of the leaves ..... *C. neesiana* var. *meylanii*

5. Leaf-apices narrowly truncate-rounded or truncate-retuse, margined by 1-2 rows of cells obviously more elongate than the interior cells; leaf-shape obliquely elliptical, usually widest a little above base or near middle; rhizoid-initial region strongly transverse, narrowly elliptical; oil-bodies absent from cells of central portion of leaf ..... (*C. neesiana*, typical)[10]

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10 Müller (1947) has synonymized Buch's *C. meylanii* with *neesiana*. I find that all American material examined is reasonably homogeneous as regards the characters used by Buch to separate it from *neesiana*. I am not yet convinced, however, that *meylanii* is fully specifically distinct from *neesiana*, and therefore tentatively treat it as a variety. I cannot, however substantiate Müller's claim (1947, p. 428-429) that *meylanii* totally lacks validity.

C. TRICHOMANIS (L.) Corda

Frequent to common. TOMPKINS CO.: Fall Creek; Enfield Glen; Coy Glen; Sixmile Creek Ravine; Sixhundred Ravine; Buttermilk Glen; Ringwood Swamp; Headwaters Swamp; Michigan Hollow Swamp; northeast of Slaterville Springs; Taughhanock Gorge; Cascadilla Ravine. TIOGA CO.: Richford; southern part of Headwaters Swamp. SENECA CO.: woods, along old roads, near Junius Bogs. GENESEE CO.: Bergen Swamp. MADISON CO.: Chittenango Falls; Unadilla Forks. ONONDAGA CO.: White Lake, Dewitt; Manlius (Goodrich 1912, p. 23). ALLEGANY CO.: Centerville (Underwood & Cook, Hep. Amer. No. 15, labelled "Centreville").[11] CATTARAUGUS CO.: Allegany State Park. MONROE CO.: Irondequoit Bay. ONTARIO CO.: Briggs Gully, Richmond. CHENANGO CO.: Bog near S. Plymouth Pond (Reservoir), S. Plymouth.

This is one of our most common species of *Calypogeia*, occurring predominantly on moist, shaded, loamy or sandy-loamy banks on circumneutral soils; apparently with only a slight tolerance for lime. Also found on disintegrating shale talus and talus slopes, associated with such species as *Cephalozia bicuspidata* and *Scapania nemorosa*. Occurring rarely in swamps and there often atypical, with the leaves more decurrent and the amphigastria more deeply divided, thus approaching the "var. *tenuis*," i.e. *C. sphagnicola*. On loamy banks it is usually accompanied by *Cephalozia media*, occasionally by *Scapania nemorosa*. Occurring occasionally with *C. neesiana* (Briggs Gully), but generally remaining perfectly distinct from it.

The non-emarginate leaves, that are as wide as long, but little decurrent on their posterior margins, and the relatively narrow underleaves, usually divided at least ½-⅔, that lack any indication of lateral teeth characterize this species (Pl. 2, fig. 14).

Usually separated specifically is the following form, which differs essentially in the colorless oil-bodies and in the shape of the amphigastria; in the area covered it appears to intergrade so perfectly and imperceptibly with *trichomanis* that treatment as a variety or form is perhaps more justifiable.[12]

C. FISSA (L.) Raddi

Infrequent. TOMPKINS CO.: Fall Creek, *Schuster;* Ringwood, *Schuster;* two miles south of Dryden, *R. M. & O. M. Schuster;* Taughannock Gorge, *Schuster*. ONTARIO CO.: Briggs Gully, Richmond, *Schuster*. CATTARAUGUS CO.: St. Bonaventure (Boehner 1943, p. 11) "At times this seemed to approach *Calypogeia sullivantii* Austin."

Occurring under identical conditions as typical *trichomanis*, but apparently absent from the occasional stations on decaying logs on which *trichomanis*

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11 At least the specimen in the University of Minnesota herbarium, of this number, should be listed under *C. neesiana* var. *meylanii*, to which it undoubtedly belongs. The collection came from a swamp, under *Thuya:* a site at which *neesiana* var. *meylanii* is usually common but where true *C. trichomanis* is usually absent.

12 Buch (1936) on the basis of culture experiments maintains them as distinct species. It cannot be denied, however, that the two approach each other closely, and appear to be connected by intermediate forms. I retain them here as species out of regard for the opinion of other workers, rather than of any conviction on my part. Müller (1947) points out that the oil-bodies in *fissa* are colorless, in *trichomanis* (unlike in any other of our *Calypogeia* species) distinctly bluish. The latter appears to be the most significant difference between the two species, and indicates two distinct species are at hand.

has been found. Occurring almost always on moist, shaded, loamy banks, more rarely on rather wet, shaded, steep disintegrating talus, with *C. neesiana* and *trichomanis* (Briggs Gully).

Usually given as a species by modern authors. The short-emarginate condition of the leaf-tips has been stressed as a species-character; I find that in local material the leaf-tips are more frequently entire and acute than bidentate; furthermore, lax forms of typical *trichomanis* often have the leaf-tips bidentate on occasional leaves. The shape of the amphigastria (Pl. 2, fig. 12) seems to me a much more constant and valuable character, taxonomically; it is apparently less dependent upon nutritional differences than is the condition of the leaf-tips. In *trichomanis* they apparently never have broad, rounded lateral lobes or teeth and are usually not shorter than wide; in *fissa* they usually approach twice as wide as long, are much more deeply divided, with a broad obtuse sinus, rather divaricate lobes, each of which usually has a broad rounded tooth on the outer side. Occasionally some of the amphigastria lack one or both of the lobes, but most stems exhibit a majority of amphigastria that are normally developed. The lateral leaves, furthermore are usually distinctly longer than wide and more or less elliptical in form (Pl. 2, fig. 12) while they are as broad or broader than long in *trichomanis* (Pl. 2, fig. 14) though they may be considerably narrower and bidentate at the tip in poorly developed shoots of the latter species. Such shoots have given rise to much confusion between the two species.

Dried material of *fissa* cannot always be kept separate from the mod. *laxifolia-dentistipula* of *trichomanis*. The latter, apparently a swamp and shade form with more remote leaves, tends to have the leaves narrowly ovate, much longer than wide, and the underleaves armed on each side with an obtuse to sharp tooth. A collection of such a lax form of *trichomanis* is before me from Chittenango Falls, Madison County, and bears numerous capsules. The capsule-valves (on five capsules studied) vary from 7.1, 7.7, 7.7, 8.5 to a maximum of 8.75 times as long as wide, thus agreeing nearly with the measurements given for *trichomanis* by Müller (1947). It is therefore evident that care must be exercised in determining material of *fissa* since lax forms of *trichomanis* may resemble it closely. The capsule-valves of *fissa* (8-13 times as long as wide), and the colorless oil-bodies are the most constant characters for separating this species from *trichomanis* (capsule-valves normally 7-9 times as long as wide; oil-bodies bluish).

C. MUELLERIANA (Schiffn.) K. Müller

Frequency unknown. TOMPKINS CO.: northern part of Headwaters Swamp, *R. M. & O. M. Schuster*. TIOGA CO.: southern edge of Headwaters Swamp, *R. M. & O. M. Schuster*. CHENANGO CO.: Plymouth Bog, *Schuster*. CATTARAUGUS CO.: Allegany State Park, *Schuster & Pendleton*. GENESEE CO.: Bergen Swamp, *Schuster & Winne*.

This species is here first reported from North America. It is, according to Müller, relatively frequent in Europe (he reports it from Norway, Germany, Finland, Switzerland, Holland), but had been confused with both *neesiana* and *trichomanis*, as well as to a lesser degree with other species. The species has an apparently wide ecological amplitude and occurs from rather dry sites to bog holes.

Müller (1947) assigns this species relatively strict limits. It is supposed to be less closely related to *neesiana* than to *trichomanis,* and differs from *trichomanis* in the colorless oil-bodies, as well as broader (and usually larger) amphigastria whose lobes are broadly rounded. The differences from *trichomanis* are apparently more readily apparent and less subject to overlapping than those existing between *neesiana* and *mülleriana.* The latter supposedly has more or less decurrent underleaves, with the cells about 25 x 50-80 μ in their middle, and with the lobes more distinct, separated by a rectangular or acute, short sinus. In material from some of the above stations many plants could not be definitely referred to either species because the underleaves varied from subentire (the usual condition, as in *neesiana*) to shortly incised, were alternately non-decurrent or slightly decurrent basally, and had the cells varying from 24-27 x 38-48 μ, with only occasionally, cells 48-64 μ long. *Mülleriana,* like *trichomanis,* is characterized by the ovate-pointed leaves that are as wide as long (Pl. 2, figs. 6-8); in the material at hand most plants had the leaves decidedly narrower than long and rounded at the apex (much as in the *Meylanii*-like form of *neesiana*); other plants had the leaves fully as wide as long and ovate-pointed, as in typical *mülleriana.* Many plants had the cells of the leaf-middle only 38-48 μ long x about 35-38 μ wide (thus scarcely or no larger than in material of typical *neesiana* seen), while some plants had the median cells about 38-40 μ wide x 48-75 μ (occasional ones to 85) long (as typical for *mülleriana*). The rhizoid initial field was generally rather broadly ovate (i.e., of the "*meylanii*"-type).

The above measurements are given in some detail to show that the cell-measurements given for the underleaves and leaf-middle by Müller do not allow as sharp a separation as indicated by his key (1947, p. 420-421). Some individual plants examined agree very closely with plants kindly sent to me by Dr. Müller, labelled by him *C. mülleriana,* and cannot be referred elsewhere because of the fact that the lateral leaves are fully as wide as long and ovate-pointed. Other plants studied are referred on a following page to *neesiana* var. *meylanii,* from which they cannot be separated. Between these two extremes are some plants whose disposition seems impossible from dead material.

It has been shown by Elwein that the size of the cells in *trichomanis* becomes larger as nutritional factors approach the optimum. This suggests that Müller has laid too much stress on the cell size in differentiating species. The immense variability of the cell size of members of this complex makes this a doubtfully useful and valid character.

C. SPHAGNICOLA (Arn. & Perss.) Warnst. and Loeske

Rare and local, perhaps overlooked. GENESEE CO.: Bergen Swamp, on Sphagnum hummocks, *Schuster & Winne.* CATTARAUGUS CO.: among peat mosses in Bog near Crystal Lake, near Freedom (*Boehner;* det. Schuster); over *Sphagnum* in Waterman Swamp, Napoli (Boehner 1943, p. 11), not seen by writer. SENECA CO.: Junius Peat Bog, *R. M. & Erwin Schuster.*

This species, very variously treated by different recent workers, is one of the index members of the *Mylia* Associule. It is confined strictly to *Sphagnum* bogs locally but in the north may occur with *Mylia* and *Odontoschisma elongatum* on peaty banks over ledges. The species is a decided calciphobe

occurring in Bergen Swamp, for instance, only on the uppermost parts of peat hummocks, where it grows rather completely shielded from the marl beneath. The pH range is from about 3.5-4.5. Most commonly associated are *Cladopodiella, Cephaloziella elachista* (and the closely related *subdentata*), and such *Cephalozia* species as *connivens* and *pleniceps*.

Since the relationship of *C. trichomanis* var. *tenuis* (=*paludosa* Warnst.) is still in question, it may not be out of place here to stress that the disposition of the latter as a modification of *sphagnicola* is certainly correct. The thickness of the cell-walls and development of the trigones of the leaf-cells is very much correlated with exposure and water availability. At places like Junius Bogs where the species occurs under often somewhat shaded, very hygric conditions, the leptodermous form *(tenuis)* prevails and no material with well-developed trigones could be found. On the crests of the peat hummocks at Bergen Swamp, however, all transitions from thick-walled, pachydermous typical *sphagnicola* to leptodermous *tenuis* could be found.

This (except for the very different *C. neesiana*) is our only species occurring in sphagnum bogs; it is also much smaller than our other species (shoots only 1-1.8 mm wide, as compared with 1.6-3.5 mm for our other species). The very small cells (those of the leaf tips mostly well under 30 μ) are diagnostic (Pl. 2, figs. 10-11).

C. NEESIANA (Mass. & Carest.) Müller var. MEYLANII Buch

Frequent. TOMPKINS CO.: northern part of Headwaters Swamp, *R. M. & O. M. Schuster;* Michigan Hollow Swamp, *Schuster & Clausen.* TIOGA CO.: southern part of Headwaters Swamp, *R. M. & O. M. Schuster.* GENESEE CO.: Bergen Swamp, *R. M. & O. M. Schuster.* ONONDAGA CO.: Jamesville (Underwood, 1890), with *L. incisa* and *J. autumnalis.* ONTARIO CO.: Briggs Gully, Richmond, Schuster. CHENANGO CO.: outlet of Plymouth *Sphagnum* Bog, S. Plymouth, *Schuster & Winne.* CATTARAUGUS CO.: in *Sphagnum* bog at Watermans Swamp, Napoli (Boehner 1943, p. 11). ALLEGANY CO.: "Centreville" (as *Kantia trichomanis* in Underwood & Cook, Hep. Amer. No. 15, with *Blepharostoma*).

Moderately distinct locally from *C. trichomanis*; in fact occurring with it (Brigg's Gully), and not exhibiting any signs of intermediate forms. Evidently much more worthy of specific recognition than is *C. fissa.*

Characterized by Ammons (1940) as a xerophyte, and by Müller as xerophytic-mesophytic, I find the species to be decidedly more meso-hygrophytic locally than xerophytic. Under meso-xerophytic conditions generally replaced by either *trichomanis* or *fissa.* Study of the above records reveals that the species occurs chiefly in swamps; when occurring in ravines as in Briggs Gully, it grew on moist to wet, very steep, shaded, north-facing disintegrating shale banks with such hygrophytes as *Cephalozia bicuspidata* as well as *Calypogeia trichomanis* and *fissa, Diplophyllum apiculatum* and the very rare *Jungermannia caespiticia.* Very evidently tolerating lime, more so than our other species of *Calypogeia,* but often decidedly humicolous, occurring on humus-rich hummocks in swamps and on very decayed logs; characteristically accompanied both on logs and humus as well as on thin humus of steep shale talus, by *Lophozia incisa* and *Jamesoniella autumnalis,* as at Bergen Swamp, Jamesville, and Briggs Gully. The species occurs very abundantly

at Bergen Swamp, more frequently indeed than elsewhere in our region. This may indicate that the species is somewhat calciphilous. Müller (1905-1916, p. 241) called attention to the fact that it prefers sandstone when occurring on rocks at all. Local distribution establishes it as rather frequent on calcareous or subcalcareous shales and sandstones. The ecological amplitude of this species is certainly greater locally than that of our other forms. In addition to the above, more frequent occurrences, the species is locally abundant with *Moerkia hibernica* and *Riccardia pinguis* and *multifida* on thin humus over marl or with *Lepidozia setacea* and *Mylia anomala* and *Cephaloziella subdentata* on *Sphagnum* hummocks over marl or as scattered hygrophytic modifications among *Sphagnum* in bogs; frequently the species occurs on very decayed, moist or wet stumps and logs — there often accompanied by *Odontoschisma denudatum*. Truly xerophytic modifications of this species are rare (at least locally) while hygrophytic modifications occur much more frequently than in the *trichomanis* complex.

A hand lens will generally separate this species from our other forms of *Calypogeia* since the very large, rotundate to broad-oval, scarcely or not retuse amphigastria (Pl. 2, fig. 13) are very different from the smaller bilobed ones of all our other forms; the leaf-apices are more rounded, and never exhibit any tendency to produce narrowly bidentate leaves, while such a tendency occurs in both *fissa* as well as in poorly developed, impoverished forms of *trichomanis*. Evidently a much less generalized species than *trichomanis* and our other species of *Calypogeia*. For the differentiation from the difficulty separable *C. mülleriana* see under the latter.

Müller (1947) stresses the smaller cell-size of the *neesiana-meylanii* complex as one of the characters separating it from the *trichomanis-mülleriana* complex. In the former the median leaf-cells are given as "35 x 40 μ", the underleaf cells as 30-40 μ long; in the latter complex they are supposedly 40 x 50-60-90 μ in the middle of the leaf while the underleaf cells are supposedly 50-80 μ long. If this is rigidly interpreted, material collected in Bergen Swamp with totally entire underleaves and ovate leaves that are about as wide as long, would key out to *mülleriana*. The general appearance of the plants suggests a broad-leaved form of *meylanii*, and the very large underleaves (2.2-3 times as wide as the stem) are entire or merely retuse. The leaf-cells however average (when short rows are measured) from 48-50-54-58 μ (a few to 76) long x 38-42 μ wide. In another leaf similar measurements gave 54-56-63 μ long x 38-45 μ wide. Median cells of the underleaves averaged 50-51-51-58 μ long x 26-28-32 μ wide.

This suggests that *mülleriana* (if the above plants are to be considered *mülleriana*) possesses a wide amplitude of variation in the shape of the underleaves. Suggestively, several other collections from Bergen Swamp show underleaves incised from 1/8-1/4, approaching more typical *mülleriana*. On the other hand, material of *mülleriana* from Plymouth Bog had almost uniformly emarginate underleaves (a few merely retuse, one totally entire), while material from Allegany State Park had all of the underleaves incised by a narrow sinus for 1/4-2/5 their length. It is readily apparent then that *mülleriana* underleaves range from a *meylanii* extreme to a *trichomanis* extreme. This

amplitude of variation in *mülleriana* is perhaps the strongest argument in favor of its specific validity. It also demonstrates that much of the material will have to be determined by carefully weighing all of the characters of the plant in question. This extreme variation in underleaf-shape explains, in part at least, why *mulleriana* as a species had been partly placed in *neesiana*, partly in *trichomanis* (Müller, 1905-1916).

Another source of difficulty lies in variations in the size of the oil-bodies. Müller (1947) gives the oil-bodies as "to 5-7 μ long" in the *neesiana-meylanii* complex, supposedly differentiating it from the *mülleriana-trichomanis* complex in which they are "to 12-14 μ long." In all examined North American material of the *neesiana-meylandii* complex (I have seen living material only of *meylanii*) the oil-bodies attain a much greater maximum size than indicated by Müller. Most commonly they are from 4 x 5-9 μ to 5 x 7.5-10 μ (and consist of 3-4 to 8 oil-globules), but in many cells they attain a size of 5 x 15 μ (exceptionally 5.5 x 18 μ and consist of 11-12 oil-globules 1.8-3.2 μ in size). It is therefore fairly evident that the oil-bodies in American material are consistently larger than indicated by Müller and may even attain a size larger than indicated for the *mülleriana-trichomanis* complex. This suggests that either North American material of the form identical in gross features with *meylanii* is genetically discrete from European material, or that the amplitude of variation in oil-body size is considerably greater than indicated by Müller. Since all of the many plants studied, from diverse localities, agreed in the large maximum size attained by the oil-bodies, it would seem that we perhaps have a discrete Nearctic race. All of this material, identical in gross features with *meylanii*, tends to have the leaf-cells 35-38 x 38-46 μ in the leaf-middle and has uniformly entire underleaves, while the lateral leaves are longer than wide and obliquely ovate (generally clearly widest basally). There can therefore, be no question about the plants belonging to the *neesiana-meylanii* complex. All of these plants also had oil-bodies well developed in the middle of the lateral leaves.

Family CEPHALOZIACEAE

I. CEPHALOZIA Dumort.

KEY TO SPECIES[13]

1. Leaves decidedly ovate, slightly to distinctly longer than wide, bifid 1/2 - 3/5 the leaf-length, the lobes narrowly triangular, not or only slightly connivent (Pl. 3, figs. 4-5) leaf-insertion quite oblique to subtransverse, not decurrent; cells 40-70 μ, pellucid, thin-walled; perianth-mouth crenulate or shortly dentate, with teeth no more than 2 cells long (Pl. 3, fig. 6); monoecious; ♀ bracts deeply bilobed (Pl. 3, fig. 4) 2

2. Flagellae present; perianth on end of very short branch; cells of leaf-middle mostly 36-45 μ; leaves of sterile shoots mostly 12-14 cells wide ..... *C. bicuspidata*

2. Flagellae absent; cells mostly 40-70 μ; leaves of sterile shoots mostly 14-16 cells wide; perianth usually at apex of long shoot, bearing vegetative leaves ..... *C. lammersiana*

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13 Vegetative characters are stressed since sterile material occurs so frequently. Occasional sterile specimens are indeterminable.

1. Leaves orbicular or suborbicular (Pl. 3, figs. 2, 7, 8-9, 11), as wide or wider than long; sinus descending 1/3 - 1/2 leaf-length, the lobes mostly broadly triangular, often connivent (Pl. 3, figs. 2, 7); leaves nearly horizontally inserted or slightly oblique, from scarcely to longly decurrent at base 3

3. Cells extremely large, 45-70 μ in leaf-middle, thin-walled (Pl. 3, fig. 2); leaves with lobes connivent, merely 3-5 cells wide at base the entire leaf only 7-9 cells wide; leaves strongly decurrent (Pl. 3, fig. 2); stolons or flagellae absent. (Perianth ciliate-laciniate at apex (Pl. 3, fig. 1); bracts 2/3 - 3/4 divided into 3-5 narrow, lanceolate lobes (Pl. 3, fig. 3); monoecious ..... *C. connivens*

3. Cells smaller, 16-35 (45) μ in leaf middle (if over 35 μ, stolons present); lobes 5-9 cells wide at base, leaves mostly 10-25 cells wide. (Perianth mouth crenulate at apex, or bracts bilobed, with lobes ciliate-dentate; bracts with 2, rarely 3 broad, triangular lobes) 4

4. Stolons present (Pl. 3, fig. 8, s); cells of leaf-middle 33-40 μ (occasionally to 50 μ), thin-walled; monoecious (Pl. 3, fig. 8); perianth-mouth crenulate by projecting cells; bracts with 2 (rarely 3) broad, entire lobes; perianth firm, 2-3 cells thick below; leaves 12-25 cells wide, non-decurrent, with nearly non-connivent lobes (Pl. 3, fig. 9) ..... *C. pleniceps*

4. Stolons absent; cells of leaf-middle 16-35 μ; dioecious; perianth unistratose throughout 5

5. Leaves not or scarcely decurrent (Pl. 3, fig. 11), with lobes little or not connivent, the sinus descending about $\frac{1}{2}$ the leaf-length; leaves mostly 12-25 cells wide, with ventral lobe often 6-9 cells wide (Pl. 3, fig. 11); perianth mouth ciliate with cilia 2-4 cells long; ♀ bracts with lobes dentate or ciliate-dentate (Pl. 3, fig. 10); leaf-cells 16-30 μ (rarely to 35 μ) 6

6. Cells 16-23 μ in leaf-middle, thick-walled; ♀ bracts 1/3 - 2/5 bilobed; androecia in short spikes, the bracts not larger than leaves; on decaying logs ..... *C. catenulata*

6. Cells 23-30 μ, rather thin-walled (Pl. 3, fig. 11); ♀ bracts 1/2 - 3/5 divided (Pl. 3, fig. 10); androecia often forming large, long spikes, with bracts larger than leaves;[14] among *Sphagnum* in bogs ..... *C. macrostachya*

5. Leaves strongly decurrent, with strongly connivent lobes, separated by a nearly circular sinus descending 1/4 - 1/3 the leaf-length (Pl. 3, fig. 7); leaves mostly 8-12 cells wide, the ventral lobe mostly 4-6 cells wide; perianth mouth merely crenulate by projecting cells; ♀ bracts with lobes entire; leaf-cells 25-35 μ ..... *C. media*

C. BICUSPIDATA (L.) Dumort.

Infrequent or scarce. TOMPKINS CO.: Taughannock Gorge, abundant, *Schuster, Andrews;* Sixmile Creek Ravine, on wet rotting log with *Riccardia latifrons* and *Nowellia, Schuster;* Sixhundred Ravine, on wet, shaded rocks, *Andrews, Schuster.* CHENANGO CO.: Plymouth Pond (Reservoir), S. Plymouth, among *S. paludicola* and *Cladopodiella* on decaying log, *Schuster & Winne;* on wet peaty edge of outlet of Plymouth Bog outlet, with *Harpanthus, Schuster & Rader.* ONTARIO CO.: Briggs Gully, Richmond, *Schuster.* GENESEE CO.: Bergen Swamp (Day 1882, p. 166, as *Jungermannia bicuspidata*); rotting log at Bergen Swamp, *R. M. & O. M. Schuster.* ONONDAGA CO.: Jamesville Road (Goodrich 1912, p. 22). CATTARAUGUS CO.: "wet loamy soil along the banks of the South Branch of Cattaraugus Creek, near Gowanda" (Boehner 1943, p. 12); Gowanda, with *Plectocolea crenulata, Boehner* (det. Schuster).

This species occurs in our area almost exclusively as a mesohygrophyte, most abundantly and characteristically as a chasmophyte and over wet ledges, or on wet talus (either directly on rock-fragments, or on the clayey soil resulting from its disintegration), where it is obviously an initial invading species

14 In all material seen from our area, however, with small androecia not different from those of *catenulata.*

of the *Cephalozia bicuspidata-Calypogeia trichomanis-neesiana* Associule. It may here occur associated with *Gymnocolea inflata, Lophozia ventricosa, Scapania mucronata,* and such northern vascular species as *Primulla mistassinica.* It is also occasional along streams (Plymouth Bog and Cattaraugus Creek) associated with *Harpanthus* and *Calypogeia trichomanis* and *neesiana,* and may occur on decaying logs in bogs (Bergen and Plymouth Pond) as a member of the mesohygrophytic *Cephalozia-Lophozia porphyroleuca-Riccardia* Associule. The species has only a slight lime tolerance but a considerable tolerance for direct sunlight if there is abundant water.

The nearly symmetrical, deeply bilobed, distinctly obliquely inserted leaves (especially of sterile shoots) which are not at all decurrent, are characteristic (Pl. 3, figs. 4-5). They are ovate in shape and have narrow, triangular-pointed lobes. The very large leaf-cells and the shortly dentate perianth mouth (Pl. 3, fig. 6) are also characteristic. In all of these characters the species differs from other species of *Cephalozia,* except from *C. lammersiana.* The distinction between *bicuspidata* and *lammersiana* are discussed under the latter. Since these two closely related forms have in the past been considered identical (and treated under the older name *bicuspidata*), many of the earlier records are unreliable. Some of the stations cited above may possibly belong to *lammersiana.*

C. LAMMERSIANA (Hüben.) Spruce*

Apparently rare locally. CATTARAUGUS CO.: "along the banks of the south branch of Cattaraugus Creek, near Gonawanda" (Boehner 1943, p. 12), det. by L. Clark. ONTARIO CO.: Briggs Gully, Richmond, *Schuster.*

This species, not generally differentiated in America from the closely related *C. bicuspidata,* must be accorded species rank because of the distinct chromosome complement. The occurrence and requirements of the species are similar to those of *C. bicuspidata* as far as known, except that the present species apparently does not appear able to invade the xeric or subxeric habitats occasionally frequented by *bicuspidata.*

The material from Briggs Gully is doubtfully placed here. The plants occurred on a moist, north-facing ravine wall, on shale talus, with *Jungermannia caespiticia.* The plants had the perianths on long shoots and lacked stolons.

The larger size of the cells (frequently 40 x 50-60 μ), absence of stolons and the usual occurrence of the female inflorescence on a long, leafy branch, separate this form from *bicuspidata* to which it is otherwise very similar in the oblique, non-decurrent leaves, shortly denticulate perianth mouth, bifid bracts, and autoecious inflorescence. In the writer's experience material of *bicuspidata* from hygric situations frequently quite or virtually lacks stolons; such material also usually has larger cells, up to about 40-50 μ. It is very difficult to place such specimens correctly, especially since the occurrence of the perianth on a long branch in *lammersiana* is not at all constant. For this reason, the species recently has been considered a mere variety of *bicuspidata.*

C. PLENICEPS (Aust.) Lindb.

Apparently rare, local. TOMPKINS CO.: northern part of Headwaters Swamp, doubtful material, *R. M. & O. M. Schuster.* SENECA CO.: Junius Peat Bog, near W. Junius,

* See Appendix, p. 703.

R. M. & Erwin Schuster. CHENANGO CO.: Plymouth Pond, S. Plymouth, *Schuster & Winne.* GENESEE CO.: Bergen Swamp, among *Moerkia flotowiana* and *Fissidens* sp. over thin layer of humus, impregnated by underlying marl, *Schuster & Winne.* TIOGA CO.: southern part of Headwaters Swamp, *R. M. & O. M. Schuster.* CHEMUNG CO.: Bog 1 mile northeast of southwest corner of county, *Schuster, Rader, & Smith.*

This species appears to be confined locally, to peat and marl bogs under more or less shaded conditions. The material examined is mostly referrable to the hygrophytic modification (variety?) of bogs, the "var." *macrantha* (Kaal. & Nichols.) Müll., since the cells are often 40-50 μ in the leaf-middle, the female inflorescence occurs occasionally on elongated leafy branches (or may even appear terminal on a main shoot), amphigastria often occur, and the perichaetial bracts are divided 1/2-3/5 or more. This form is usually readily distinguishable but appears to be essentially a form induced by a more ample and constant water supply. In much of the material examined flagellae (stolons) were very rare or virtually absent — perhaps also a modification induced by more ample water supply. The species is generally considered calcifugous but this is not always true since at Bergen the species occurred with such pronounced calciphiles as *Moerkia, Riccardia pinguis* and *Lophozia rutheana.* Most frequently the species occurs in the later stages of the *Sphagnum*-Sedge Mat Associes, or the *Chameadaphne* Heath Associes. In its earlier stages it is a typical member of the *Mylia* Associes, but persists long after all other members of the *Mylia* Associes have been shaded out, and may indeed persist into the Pine-Hemlock-Yellow Birch Subclimax.

Several of the above collections, as indicated, are referred here tentatively only, since flagellae could not be demonstrated. There is little doubt about their determination however, since in each case the 2-3 stratose perianth-wall eliminated all other species.[15]

The distinctly crenulate mouth of the perianth (Pl. 3, fig. 8), which is 2-3 cells thick below, the bilobed bracts with entire lobes, the large leaf-cells, and the monoecious inflorescence are quite diagnostic even if stolons cannot be found. If flagellae are demonstrable, they at once eliminate all other species except the otherwise very different *C. bicuspidata.*

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15 Müller (vol. 2, pp. 32-33) discusses briefly the *Cephalozia bicuspidata* var. *capitata* Eckstrand (*C. Eckstrandi* Limpricht), one of the most distinctive features of which is the presence of small, globose heads, formed by transversely inserted malformed leaves that bear gemmae. This var. was placed by Müller as a form of *C. pleniceps,* apparently justly so. Two of the collections at hand (that from Junius and the one from Chemung Co.) closely approach the var. *capitata;* both bear abundant small, globose heads, formed mostly by two nearly opposite subtransverse leaves, between which the apex of the stem (and unrecognizable malformed terminal leaves) are highly proliferous, giving rise to branched masses of cells, some of which mature into bright green gemmae, oval to ellipsoidal or somewhat pyriform in shape, 16-24 x 12-14 μ in diameter. According to Müller this var. has the leaves averaging about 20 cells wide, directed forward and concave in form. The present hygrophytic modification closely agrees with Müller's description but is decidedly larger in size (approaching var. *macrantha*); unlike the var. *macrantha* the cells are relatively small in the leaf-middle (averaging 34-38 μ) and the larger leaves average 24-25 cells wide or even more. The presence of many such leaves, each consisting of well over 150 cells, separates *pleniceps* from all our other species except *macrostachya* which has rather similar, many-celled leaves but with considerably smaller cells.

C. CONNIVENS (Dicks.) Lindb.

Frequent to common, but local: CHEMUNG CO.: Bog 1 mile from southwest corner of state. TOMPKINS CO.: McLean Bogs, among *Sphagnum;* Woodwardia Bog; Malloryville Bog; Headwaters Swamp; Michigan Hollow Swamp; Ringwood. CORTLAND CO.: Beaver Brook, near South Cortland, on a log. GENESEE CO.: Bergen Swamp. CATTARAUGUS CO.: "Common in swamps and bogs" (Boehner 1943, p. 12); Waterman Swamp, in deep bog *Sphagnum,* Boehner (det. Schuster). SENECA CO.: Junius Peat Bogs. CHENANGO CO.: Plymouth Pond, S. Plymouth, on rotten logs with *Odontoschisma* and *Lophozia porphyroleuca,* etc. *Schuster & Winne;* Plymouth Bog, *Schuster & Rader.*

This species occurs almost exclusively in bogs and marshes, growing on soil, very rotten logs, or among mosses, especially *Sphagnum.* In *Sphagnum* bogs where it is the characteristic *Cephalozia,* it grows with *Cephaloziella elachista, Mylia anomala, Cladopodiella fluitans,* and rarely with *C. pleniceps.* The species is more distinctly hygrophytic than our other common local species but often occurs in well exposed areas as in open bogs. It does not appear to be a distinct "calciphobe," occasionally occurring in marl bogs.

The ciliate-laciniate perianth mouth (Pl. 3, fig. 1), narrowly lanceolate lobes of the deeply 3-4-fid perichaetial bracts (Pl. 3, fig. 3), and the monoecious inflorescence easily distinguish the species. The very large leaf-cells (45-50 or more μ) separate the species from our other forms except *lammersiana* (Pl. 3, fig. 2).

C. MEDIA Lindb.

Common: TOMPKINS CO.: Slaterville Springs (Sixhundred Ravine); n.e. of Slaterville; Sixmile Creek; Ringwood; Enfield Glen; Coy Glen; McGowans Woods near Varna; Fall Creek; Cascadilla Creek; Freeville; West Hill woods. CORTLAND CO.: Truxton; West Hill Woods. GENESEE CO.: Bergen Swamp. MADISON CO.: Chittenango Falls. TIOGA CO.: southern part of Headwaters Swamp. ONONDAGA CO.: Pompey; White Lake, Jamesville; (Onondaga) Valley (Goodrich 1912, p. 22, as *C. multiflora*); Syracuse. CHEMUNG CO.: Van Etten (No. 1, Hep. of the Upper Susquehanna, Barbour); Bog 1 mile from southwest corner of county. CHENANGO CO.: on rotten wood along bog outlet of Sphagnum bog, S. Plymouth, *Schuster, Winne & Rader.* CATTARAGUS CO.: Waterman Swamp, Napoli; Lime Lake; Bonaventure (Boehner 1943, p. 12); Steamburg (Knobloch 1934, p. 10); Olean Rock City.

This is our most widespread local species: it occurs most commonly on rotting logs, often with *Nowellia,* but may occur on shaded, often somewhat loamy soil, on logs in woods, there associated with such species as *Blepharostoma trichophyllum, Calypogeia trichomanis,* etc. The species is a distinct mesophyte, and tolerates but very little direct light, growing very rarely on soil on the exposed crest of ravines, such as of Fall Creek.

The dioecious inflorescence, the strongly decurrent circular leaves (Pl. 3, fig. 7), with a shallow sinus and strongly connivent lobes, the crenulate-mouthed perianth and bilobed perichaetial bracts abundantly characterize this species.

C. CATENULATA (Hübn.) Spruce

Scarce locally: TOMPKINS CO.: Slaterville Springs, just below Sixhundred Ravine; Enfield, *Wiegand.* CORTLAND CO.: Beaver Brook, near South Cortland, *Andrews.* CATTARAUGUS CO.: Mt. Moriah, Vandalia; Conewango Swamp, Leon (Boehner 1943, p. 12). GENESEE CO.: Bergen Swamp, *Schuster & Winne.*

This species, like *C. media,* usually occurs on rotting logs that are somewhat

moist but not wet. It is a rather uncommon member of the *Nowellia-Jamesoniella* Associule of firm rotting logs, closely associated with *Lophocolea heterophylla, Nowellia, Cephalozia media,* etc. The species is apparently "calciphobous," since it never appears to occur away from rotting logs locally; away from the area here treated it has been reported also on acid soils and non-calcareous, moist rocks.

The small cells and dioecious inflorescence ally this species to *C. media*; the more deeply bilobed, scarcely decurrent leaves and the short-ciliate perianth-mouth easily separate it from that species. The thick-walled, deep green, densely chlorophyllose cells, merely 16-24 μ separate it from all our other species of *Cephalozia.*[16]

C. MACROSTACHYA Kaalaas

Apparently very rare, possibly overlooked. CHENANGO CO.: Floating moor of Plymouth Pond, near S. Plymouth, April 1946, *Schuster & Rader.*

16 The original specimen of Hübener's *J. catenulata,* according to Müller (1905-1916, p. 779) was found on "Torfboden in Sümpfen, auf den höchsten Punkten der Eiffel (Mountains), zwischen Bonn und Trier." This material apparently has disappeared. Whether this specimen is identical with *C. catenulata* as now delimited, is very questionable for the following reasons: 1. *catenulata* apparently does not occur in bogs, but is almost entirely limited to rotting logs; 2. Shiffner (according to K. Müller) did not see Hübener's original of *catenulata,* but saw merely material Hübener afterwards assigned to *catenulata* (according to Macvicar, 1926, p. 273 Schiffner did examine the original of *catenulata*).

It is therefore possible that Hübener's *J. catenulata* actually represents part of what is now called *macrostachya.* Since this cannot be settled without reference to Hübener's original, current usage (that of Schiffner, followed by Macvicar) is followed. The description and illustrations by Frye and Clark must be partly or entirely disregarded since these writers followed Müller, who confused forms of *macrostachya* with *catenulata,* and copied his illustrations (which, had they read his "Nachträge," pp. 778-780, they would have found out to be, according to his own admission, very doubtfully referrable to the present complex). The above indicates that there has been considerable confusion between *macrostachya* and *catenulata.* In the writer's opinion, only material with spinose- or serrate-dentate perichaetial bracts should be referred to these species. I believe, that tentatively at least, all material with large cells and thin cell walls occurring in bogs and swamps, should be referred to *macrostachya* and that all material with small, thick-walled, densely chlorophyllose cells, should be referred to *catenulata.* It may be desirable to separate the material with small androecia from typical *macrostachya* as a separate variety. Critical study may indeed show that the forms of *macrostachya* with small androecia should be referred to *catenulata.* In my limited experience with the group I am more impressed with the form of the androecia, than I am with the difference in cell size and cell-wall thickness. This is especially so since I find these to be quite variable in material of *macrostachya*—some plants from a patch having the cells very thin-walled and 25-32 μ in diameter, while others from more exposed portions of the same patch, have them merely 18-24 μ, with individual cells even smaller, and have the walls slightly thickened. It is not inconceivable that such individuals should be placed with *catenulata.*

Schiffner (Hedwigia, 54: 311-321) considers the plants placed by Müller and other writers in *catenulata* that possesses entire perichaetial bracts, as a mixture of several other species. Although Frye and Clark (1937-1947, p. 493) state "at least not the female branch and bracts of Fig. 18" of Müller's illustrations are referrable to *C. catenulata,* they nevertheless inexplicably copy both Müller's Figs. 18A and 18D (their Figs. 5 and 3, respectively); their Figs. 1 and 2 also copied from Müller, come, according to Müller, from the same plant, and are therefore also to be disregarded.

This species occurs apparently without exception on and among *Sphagnum*, associated with *Mylia* and other members of the *Mylia* Associule. The distribution of the species is northern and it occurs here near its southern boundary, obviously as a disjunct, together with the equally locally relic *Scapania paludicola*.

C. macrostachya cannot always be separated with certainty from *C. catenulata*, even when fertile. In material from the above locality the cell size of most plants examined agrees perfectly with that given by the European workers as typical for *macrostachya*; other plants occur with many of the cells of the leaf-middle as little as 18 μ (with the average about 22-24 μ); some plants have the cells quite thin-walled, others with them distinctly thickened. The dentate and spinose-dentate ♀ bracts all have the sinus descending ½ or more, however, characteristic of *macrostachya*. The few male plants seen have the androecia of 8-10 pairs of bracts, with the individual bracts about equal to the leaves in size but they are not at all dentate. The material thus is quite intermediate in form between *catenulata* and *macrostachya* but since most plants have the cell size considerably larger than in the former, and since the material uniformly occurred among *Sphagnum*, it seems impossible to dispose of it other than as here done.

The dioecious nature of the species, the rather small cells (20-36 μ mostly), and the deeply bilobed and dentate to spinose-dentate ♀ bracts (Pl. 3, fig. 10) serve to identify this species. The short-ciliate perianth-mouth and little or not connivent lobes of the little decurrent leaves are also characteristic (Pl. 3, fig. 11). Critical study of the *media-macrostachya-catenulata* complex is much needed, however, before final delimitation of the latter two species will be possible.[17]

17 See discussion under *C. catenulata*. Müller (1947a) has recently gone into the question of the differentiation between the two species. He has examined the specimen of *catenulata* cited by Hübener from the Vosges Mts. (the original from moors in the Eiffel Mts. has disappeared) and finds it undoubtedly represents what we now call *catenulata* and what has been known as *reclusa*. This material has leaf-cells 15-22 x 20-25 μ in the leaf-middle. Some of the individual leaves of the material I here place in *macrostachya* have the cells no larger, on an average; other plants have them 35 μ long. This still leaves unanswered the limits that are to be assigned to the two species.

Müller (1947a, p. 37) gives the following differences between the two species, which may help in separating North American material:

	C. catenulata	*C. macrostachya*
Dorsal epidermal stem cells	20-25 x 25-35 μ	20-30 x 40-65 μ
Leaves	not decurrent	slightly recurrent
Lobes at base	3-4 cells wide	4-7 cells wide
Cells in leaf-middle	14-17 x 20-25 μ	20-25 x 30-35 μ
Occasional cells of leaf-base	25 x 33 μ	33-40 x 45-60 μ

The local material, significantly, had the dorsal cortical stem cells 43-68 μ long x 36-42 μ wide, on very large stems, with the width decreasing to 24-32 μ on many shoots. Many leaves had the bases of the lobes from 8-9 cells wide (Pl. 3, fig. 11), or even broader than indicated by Müller.

II. NOWELLIA Mitt.

N. CURVIFOLIA (Dicks) Mitt.

Abundant: TOMPKINS CO.: Sixhundred Ravine; Sixmile Creek Ravine; Coy Glen, Ringwood; Enfield Glen; Lick Brook; McLean; Malloryville Bog; Freeville Swamp; Woodwardia Bog; Headwaters Swamp; Michigan Hollow Swamp; 2-3 miles south of Dryden; Pony Hollow (Newfield); Dryden; Fall Creek. GENESEE CO.: Bergen Swamp. CHEMUNG CO.: 1 mile from southwestern corner of state; Van Etten. TIOGA CO.: Southern part of Headwaters Swamp. CORTLAND CO.: Beaver Brook near South Cortland; east of Solon; Homer Gulf in Homer. SENECA CO.: near Junius Bogs. MADISON CO.: Chittenango Falls. ONTARIO CO.: Briggs Gully, Richmond; Canandaigua. ALLEGANY CO.: Alma; Centerville (Underwood & Cook, Hep. Amer. No. 17, listed from "Centreville"). CATTARAUGUS CO.: near Rock City south of Olean. CHENANGO CO.: Plymouth Pond, S. Plymouth, and Plymouth Bog.

This species occurs without exception on rotting logs and is a dominant member of the *Jamesoniella-Nowellia* Associule. The usually associated species are *Lophocolea heterophylla, Cephalozia media* and *catenulata,* and, more unusually *Odontoschisma, Harpanthus,* and *Lophozia porphyroleuca.* The latter forms generally represent a further stage, invading decaying logs only after they have become quite soft and have started to disintegrate, a stage at which *Nowellia* begins to disappear.

The constant occurrence on rotting, shaded to rather exposed, moist logs, and the transversely inserted bilobed leaves with each lobe running out into a long cilium, as well as the strongly constricted insertion of the leaves, differentiate this species. The species has a very characteristic appearance with the leaves strongly inflated and looking like billowing sails. Under all but extremely shaded conditions the depressed mats have a decided rosy-purple appearance, unlike all related forms. Unlike all forms with which it could be confused, *Nowellia* has the ventral leaf-margin bent inward to form a sort of water-sac, like the *Lejeuneaceae.*

III. CLADOPODIELLA Buch

C. FLUITANS (Nees) Buch

Very local, but usually frequent where found: TOMPKINS CO.: McLean Bogs (bog A), *Andrews, Schuster;* Malloryville Bog, *Schuster.* SENECA CO.: Junius Peat Bogs (first collected by *Wiegand, 1916; Schuster 1945*). CHENANGO CO.: Sphagnous edges of Plymouth Pond, S. Plymouth, *Schuster & Winne.* CATTARAUGUS CO.: Waterman Swamp, *Boehner* (det. by Schuster).

This species invariably occurs in *Sphagnum* bogs or on the wet muck around their edges; it and *Mylia anomala* are the dominant members of the *Mylia* Associule of our northern *Sphagnum* bogs. Commonly associated with them are *Cephaloziella elachista, Calypogeia sphagnicola* and *Cephalozia connivens.* Probably present in all of our larger, open *Sphagnum* bogs. Decidedly intolerant of even traces of lime; with low pH preferendum.

The more or less elongate bilobed leaves with the lobes rounded at the apex, the attenuate growth with the leaves always distant, easily separate this species from all others in the region except *Gymnocolea inflata*; the latter differs in lacking stolons and in possessing entirely lateral branches. The species also differs from *Gymnocolea* in that the perianth which is on a short

ventral branch, is trigonous and elongate, not inflated, and is never caducous. Sterile material can be best separated by the leaf form, however in the *Cladopodiella* they are oval-oblong, and bilobed 1/5-1/3, with the sinus acute and narrow, and with the ventral lobe always larger than the dorsal; in *Gymnocolea* the leaf is subcircular with the lobes subequal in size. Furthermore, in *Cladopodiella* the cells are usually quite thin-walled, and 35-45 μ in size while they are usually thick-walled and only 20-28 μ in *Gymnocolea*.

IV. ODONTOSCHISMA Dumort.

KEY TO SPECIES[18]

1. Gemmiparous erect shoots with yellow-green apical masses of gemmae almost constantly present; shoots becoming narrower basally and apically; trigones very large, bulging ..... *O. denudatum*

1. Gemmae absent; shoots not prominently narrowed basally and apically; trigones large, but rarely bulging ..... *O. sphagni*

O. DENUDATUM (Nees) Dumort.

Frequent but local: TOMPKINS CO.: Michigan Hollow Swamp; Pony Hollow in Newfield; Freeville Fir Tree Swamp; Woodwardia Bog; swampy area 3 miles south of Dryden; headwaters of Sixmile Creek; Sixhundred Ravine; Sixmile Creek Ravine; Malloryville Bog; Enfield Glen; south of Michigan Hollow Swamp; Ringwood Swamp; Coy Glen. CORTLAND CO.: Beaver Brook near South Cortland. GENESEE CO.: Bergen Swamp. TIOGA CO.: Headwaters Swamp; southeast of Caroline in Richford. ONTARIO CO.: Briggs Gully and vicinity, Richmond. CHENANGO CO.: Plymouth Pond, S. Plymouth; Bog near South Plymouth. CATTARAUGUS CO.: St. Bonaventure; Chamberlain's Bog, Steamburg; Cold Spring; Mt. Moriah, Vandalia (Boehner 1943, p. 12).

Occurring almost without exception on rotting wood; found on logs in a more advanced state of decay, usually more moist or wet than those on which the *Jamesoniella-Nowelia* Associule occurs. It is not usually associated with the species characteristic of that union *(Lophocolea heterophylla, Cephalozia media, Ptilidium pulcherrimum*) but as a distinct lociule with *Jamesoniella autumnalis, Lophozia porphyroleuca, Riccardia latifrons,* etc. — species of more decayed, moister logs, usually in swamps or at the edges of brooks or ponds, where water keeps the rotting wood near the saturation point.

The erect, usually abundant gemmiparous branches, yellowish-green at the tip, even when the rest of the plant is deeply reddish-tinged, are characteristic

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18 I have found only *O. denudatum* in the region; Goodrich (1912) reports *O. sphagni* from Onondaga Co.; whether this record is correct or whether it is a misdetermination for *O. denudatum* (as was commonly the case before Evans' revision of the genus in 1905) cannot be told with certainty until the material in question can be seen.

Frye and Clark (Univ. Wash. Publ. Biol. 6 :465, 1944) confused the salient characteristics of the species, as given in their table; *O. sphagni* according to their account, does not have bordered leaves, occurs on rotten wood and rocks, bears abundant gemmiparous branches, etc., all of which is true of *denudatum,* and not of *sphagni;* under *denudatum* they indicate that the species grows among *Sphagnum,* and lacks gemmiparous shoots, etc.; they apparently have the two species confused. Their illustrations, taken in some cases from old works like that of Hooker, further increase the confusion. Those of Hooker given under *O. sphagni,* are without much doubt figures of *O. denudatum* since Fig 11 shows the typical erect, attenuate flagelliform, gemmiparous shoot of *O. denudatum* which is always absent in *sphagni.*

of the species. It is our only species commonly reddish-pigmented that bears such erect, attenuated shoots. The large, bulging trigones and ventral stolons also easily differentiate the species. Rarely as at Woodwardia Bog, the species occurs scattered among mosses on peaty ground, a habitat more often characteristic of *O. sphagni*.

(O. SPHAGNI (Dicks.) Dumort.

ONONDAGA CO.: South Onondaga (Goodrich 1912, p. 23; record doubtful).

Found mostly among *Sphagnum*, very rarely on rotting wood near such bogs. A northern species very doubtfully present in our area).

Family CEPHALOZIELLACEAE

I. CEPHALOZIELLA (Spr.) Schiffin.[19]

KEY TO SPECIES

1. Sterile leaves entire-margined, except for the simple lobes, or the backs of the leaves with cellular projections (Pl. 4, fig. 1), divided 1/2 - 2/3 (Pl. 4, figs. 7, 9); cells normally all less than 20 μ long; leaf-lobes less than twice as long as wide, not lanceolate (Pl. 5, figs. 2-3; Pl. 4, fig. 7); bracts very finely serrate-dentate to entire (Pl. 4, fig. 7; Pl. 5, fig. 1), usually connate with bracteole for about 0.3-0.7 their length; rarely in *Sphagnum* bogs 2

2. Large amphigastria present throughout on sterile, non-gemmiparous shoots, often 0.3-0.5 as large as leaves (Pl. 4, figs. 3, 10); dioecious species, almost always sterile; leaves with lobes 6-9 cells wide at base, the cells slightly to strongly thickened (Pl. 4, figs. 5, 12) 3

3. Leaves of non-gemmiparous shoots entire-margined; backs of leaves never with cellular protuberances (Pl. 4, figs. 11-12) ..... *C. byssacea*

3. Leaves of non-gemmiparous shoots dentate laterally (Pl. 4, figs. 1, 5); the backs of the leaves with coarse projections formed from 1-5 cells (present on at least some leaves) (Pl. 4, figs. 1-2) ..... *C. byssacea* var. *scabra*

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19 The species of this genus are very badly in need of revision. Some critical notes are added here but study of large bodies of material are needed to fully eliminate the chaotic condition the group was left in after the work of Douin. Far too many forms have been described on the basis of very insufficient material, and much too briefly to make their future recognition possible. In addition many intergrades between these forms have been described, not immeasurably adding to the difficulty. Müller (1947a) has in some cases cleared the situation somewhat in disposing categorically of almost all of the species and "genera" and "subgenera" of Douin.

In this regard it may not be out of place to mention that the work of Müller largely coincides with the author's conclusions. Müller, for instance criticizes Douin for creating a separate subgenus (*Dactylophyllum* for *C. sullivantii*) on the basis of the presence of 8-9 lobes in the perichaetial ring of bracts. Müller synonymizes *sullivantii* as a variety of *rubella* and lays little emphasis on the number of lobes of the bracts. In *C. subdentata* which is supposed to have a 5-6-lobed ring of bracts, I find similar variations. Four rings of bracts haphazardly selected (Pl. 6, figs. 3, 5, 9-10) show 6 lobes in one case, 7 in another, and 8 in a third, with 9-10 in the fourth.

If the continuity of organic life and the genetic diversity of even the most homogeneous species is admitted, the entire concepts that underlie Douin's work on this group must be discarded. Unless one accepts the Lamarkian approach of Douin, most of his species and varieties must be considered invalid. For a detailed critique of the previous work on the group, the paper by Müller (1947a) should be consulted.

2. Amphigastria of sterile, non-gemmiparous shoots minute or absent, never of more than 1-5 cells (Pl. 4, figs. 6-7; Pl. 6, figs. 1-2); monoecious species, usually with perianths and sporophytes abundantly produced (androecia and perianths always closely associated); leaves lack papillose outgrowths; leaf-lobes of sterile leaves 3-6 (7) cells wide 4

4. Cells 10-14 μ wide and 11-15 (rarely 16-18) μ long; lobes variable in width; and bracts squarrose, forming a stellate head; minute amphigastria usually distinct on sterile shoots; paroecious ..... *C. stellulifera*

4. Cells 10-14 μ wide and 11-15 (rarely 16-18) μ long; lobes variable in width; leaves and bracts never forming a squarrose head; amphigastria usually absent on sterile non-gemmiparous shoots 5

5. Cells more or less thick-walled; normally paroecious, the leaves below the bracts saccate and larger, more or less dentate (Pl. 5, fig. 1); leaf-lobes mostly 3-5 cells wide 6

6. Paroecious; leaf-lobes 4-5 (6) cells wide on sterile shoots 7

7. Ring of bracts 5-6-lobed; leaf-cells thick-walled and 12-15 μ (Pl. 5, fig. 3); amphigastria absent on sterile shoots ..... *C. rubella*

7. Ring of bracts 7-9-lobed; leaf-cells often thin-walled and 10-13 μ; minute amphigastria often present on sterile shoots ..... *C. rubella* var. *sullivantii*

6. Autoecious; leaf-lobes mostly 3-4 cells wide on sterile shoots, thick-walled ..... *C. rubella* var. *bifida*

5. Cells thin-walled, 11-14 μ (rarely to 18 μ long); leaf-lobes mostly 6-7 cells wide; autoecious (Pl. 4, figs. 7, 9), the androecia on separate shoots (usually appearing dioecious because of the death of the older, connecting portions of the plants) ..... *C. hampeana*

1. Sterile leaves often distinctly dentate (Pl. 5, figs. 4-5; Pl. 6, fig. 7), or more or less obscurely crenulate-dentate (Pl. 6, fig. 8) by projecting marginal cells, divided ¾ or deeper into two lanceolate lobes twice or more as long as wide at base; leaf-lobes 2-5 cells wide on sterile stems; bracts distinctly spinose-dentate, the teeth often recurved, united with bracteole for 0-0.3 their length (Pl. 5, fig. 7; Pl. 6, figs. 5-6, 9-10); cuticle often verrucose (Pl. 5, fig. 8); only in bogs and swamps; autoecious (Pl. 5, fig. 7) 7

8. Cells thin-walled, 12-20 x 20-30 μ; many leaves near base with one-several spinose teeth 1-3 cells long (Pl. 5, fig. 4); cuticle not to moderately verrucose; bracts entirely free from bracteole; leaves mostly spreading (Pl. 5, fig. 5); spores 10-11 μ, verrucose; bracts spinose-dentate or spinose-ciliate, usually with many teeth recurved (Pl. 5, fig. 7); perianth green ..... *C. elachista*

8. Cells thick-walled, often with walls pigmented, 10-13 x 12-20 μ (Pl. 6, figs. 4, 7-8); leaves not or very rarely with a distinct basal tooth, but more or less crenate-dentate by projecting cells (Pl. 6, figs. 4, 7-8); cuticle typically coarsely, prominently verrucose (Pl. 5, fig. 8); bracts mostly united 0.2-0.3 with bracteole on at least one side; leaves mostly erect or erect-spreading (Pl. 6, fig. 6); spores typically about 7-8 μ, smooth or nearly; bracts spinulose or spinulose-denticulate to serrate-dentate (Pl. 6, figs. 3, 5-6, 9-10); perianth often purplish-tinged, except for the bleached apex ..... *C. subdentata*

C. BYSSACEA (Roth) Warnst. (DIVARICATA (Franc.) Schiffn.)*

Apparently frequent. TOMPKINS CO.: Enfield Glen, on moist rocks, *R. M. & O. M. Schuster;* Taughannock Gorge, 1945, *Schuster.* CATTARAUGUS CO.: Soil in woods, St. Bonaventure, College Grounds (Boehner 1943, p. 12). ONTARIO CO.: Briggs Gully, Richmond, *Schuster.* CHEMUNG CO.: Veteran, *Schuster.*

* See Appendix, p. 703.

This species occurs on rather dry to slightly moist shale outcrops and talus or on leached, sterile ravine slopes, occasionally on moist banks. The deep green color, usually purple or purplish-black pigmented in exposed areas is characteristic. It frequently grows together with the var. *scabra* often with *Diplophyllum apiculatum, Lophozia barbata,* and occasionally with *Gymnocolea inflata.*

Under the microscope the prominent underleaves present on sterile shoots (Pl. 4, fig. 10), as well as the frequent occurrence of shoots bearing gemmae that have coarsely dentate leaf-lobes, at once separate the species. In the field the absence of brown, but often reddish, or purplish pigmentation and the usual absence of inflorescences will help to distinguish it. It furthermore occurs more commonly on rocky ground than our other common species *(hampeana* and *myriantha)* which usually occur on sandy-loamy, denuded soil and often associated with *Lophozia bicrenata.* This species and the next form have the leaf-lobes commonly 7-8 cells wide at base (Pl. 4, fig. 12), even on sterile shoots; all our other species have them 4-5 cells wide, only rarely occasional leaves with them as much as 7 cells wide.

C. byssacea var. scabra (Howe) comb. n.

C. starkii var. *scabra* (Howe) Clark and Frye; *C. papillosa* of Douin.

Apparently rare. TOMPKINS CO.: Taughannock Gorge, on moist disintegrating shale talus, 1945, *Schuster.* ONTARIO CO.: Briggs Gully, Richmond Township, 1945, *Schuster.* New to New York State.

Almost always occurring with typical *byssacea,* and usually intergrading freely with it. When typically developed, at once differing from all other forms of *Cephaloziella* in that the backs of the leaves are provided with usually several papillose out-growths, more or less conical in form, consisting of 1-5 cells (Pl. 4, figs. 1-2). Usually however, with only a small fraction of the material thus developed, the majority of plants with only occasional papillose out-growths on only occasional leaves; other plants with no papillose out-growths at all but with the leaf-margins distinctly dentate as in normal *scabra.* In some cases a portion of the stem may bear leaves grading into *scabra,* then may bear the typical papillose leaves of *scabra,* succeeded in turn by sections of the stem with the leaves approaching *byssacea.* This together with the fact that *scabra* occurs almost invariably with *byssacea* would suggest that the former represents at most a form (as I prefer to treat it tentatively) or probably only an xerophytic modification. The *byssacea*-like shoots or portions of shoots usually have larger cells and are not pigmented and have the cells appreciably smaller. The differences between the two may thus be seasonal, the *scabra*-like growth being later during the drier part of early summer, the *byssacea*-like growth being early-spring growth. It is thus questionable whether Douin's "*papillosa*" is at all a genetic variant and hence it is questionable whether or not the name should be dropped entirely. There is conceivably a genetic variant, typically bearing only papillose leaves, and a vicarious form or modification of *byssacea,* able to produce papillose leaves when the environment is conducive to their growth. Douin (Rev. Gen. de Bot., p. 310, 1916) believes that high, not low, humidity is the major cause of the

papillose leaf-outgrowths. My observations tend to the opposite view; in support I may cite the fact that *"papillosa"* typically has smaller cells with thicker walls than *byssacea* — characteristic of forms or modifications produced under conditions of lower humidity. The papillose out-growths may in fact be a modification that increases the leaf-surface and thus allows more rapid absorption of moisture by the plant. The thicker cell-walls naturally decrease the transpiration-rate; they are a normal development of all xerophytic forms. It is therefore very probable that some *"papillosa"* is no more than a pachydermous modification of *byssacea*; since there is still some doubt about this, I retain a Latin name for the plant until a study of the question of culture-methods can finally decide it. The artificiality of creating a separate "subgenus" for *"papillosa"* and its allies, distinct from the stock-form *byssacea*, as done by Frye and Clark, scarcely needs to be commented upon.

Frye and Clark cite several other differences between *byssacea* and *"papillosa."* The marginal teeth of the leaves of the latter often are nearly absent; furthermore, otherwise normal *byssacea* may show traces of them. The cell-walls of many specimens of *papillosa* bearing the papillose leaf-outgrowths are fully as thin, and the cells fully as large, as in normal *byssacea*. The epidermal stem-cells of *byssacea* may be thicker than those of some forms of *papillosa*, though the opposite is true according to Frye and Clark's table. None of the differences cited between the two by Frye and Clark therefore represent other than differences that are bridged by modifications of one and the same population, often growing within a foot of each other.

C. BYSSACEA var.

Rare. ONTARIO CO.: Briggs Gully, Richmond, on steep, moist, sheltered slope, among mosses and *Scapania nemorosa*, Oct. 28, 1945, *Schuster*.

Similar to typical *byssacea*, but with the leaves of sterile shoots with commonly a sharp tooth near the base of the postical margin, frequently with additional teeth, mostly on the ventral lobe. The underleaves are reduced in size, rarely over 36 μ long, most commonly of only two cells in a row, about 24 μ long; occasionally of 4-7 cells, acuminate-lanceolate. Lobes with the cells quite variable; on sterile shoots rather thin walled, mostly 12-14 μ x 14-16 (20) μ, but on many shoots only 9 x 12 μ. Sterile leaves widely spreading to squarrose with divaricate, lanceolate-ovate or triangular lobes; leaves of fertile shoots mostly erect, rounded-quadrate to subovate, somewhat concave with the lobes scarcely divaricate. Fertile shoots and perianths as in normal *byssacea*; the bracts decidedly spinulose, however.

This variety approaches Douin's var. *examphigastria (=subexamphigastria)* in the reduced size of the amphigastria; it somewhat approaches the var. *rupestris* in the presence of teeth of the leaf-margins but differs from it in the minute size of the amphigastria and the thinner cell-walls of the leaves. The variety differs considerably from normal *byssacea* in that the leaves on non-gemmiparous shoots are usually dentate with sharp, distinct teeth (somewhat approaching *C. elachista* in appearance), in the more variable size of the cells (generally somewhat larger), in the reduced, frequently obsolete am-

phigastria, and in the usually smaller number of cells across the lobes of sterile leaves (mostly 6, occasionally 7-8, occasionally only 5).

The confused state in which *Cephaloziella* is at present makes description of further forms a matter of doubtful value; the present variety however, appears to be a genetic form and not the result of environmental modification. The possession of sharp teeth or lobes on many of the leaves gives the plants a characteristic appearance; the small, easily overlooked amphigastria and the mostly 6, occasionally 5-cells wide leaf-lobes, as well as the squarrose leaves suggest *C. stellulifera;* this is enhanced by the frequently somewhat squarrose appearance of the immature bracts. The larger cells of the latter species, the yellowish-green color, and paroecious inflorescence distinguish it however. The present variety appears to be dioecious; antheridia could not be discovered in the axils of the subinvolucral bracts nor could separate androecia be found.

C. RUBELLA (Nees) Warnst.

Abundant. TOMPKINS CO.: South Hill near Ithaca, *R. M. & O. M. Schuster;* Six-mile Creek Ravine, *Schuster;* Coy Glen, *R. M. & O. M. Schuster;* sandy-loamy bank 2 miles south of Dryden, *R. M. & O. M. Schuster, C. Grady, M. McLeod;* Fall Creek Ravine, *Schuster;* Old Buttermilk Glen, *R. M. & O. M. Schuster;* Taughannock Gorge, *Schuster & Clausen;* McKinney's Twin Glens, *R. M. & O. M. Schuster;* Buttermilk Ravine at Treman Lake, *R. M. & O. M. Schuster;* Enfield Glen, *Schuster.* CHEMUNG CO.: Veteran, *Schuster.* SENECA CO.: sandy, sterile soil near Junius Peat Bogs, *Schuster.* ONTARIO CO.: Briggs Gully and vic., Richmond, *Schuster.* CATTARAUGUS CO.: Rock City, *Schuster & Rader.* CHENANGO CO.: exposed, sterile slope of field, S. Plymouth, *Schuster & Winne.*

This species abundantly invades denuded, sterile, acid or circumneutral soils or thin soils over shale and sandstone ledges; it prefers soils of a heavy consistency — clay or loam; occurs most abundantly under conditions of direct sunlight (in the ravine area almost constantly on the sunny, south-facing crests rather than on the south crests where most other species occur). A decided xerophyte, occurring almost constantly with *Lophozia bicrenata,* frequently with *Plectocolea crenulata,* and occasionally with *Scapania nemorosa* or *Lophozia barbata.* It occasionally occupies similar situations as xeric forms of *Ptilidium pulcherrimum* but is unable to compete with the latter because of the latter's rapid horizontal growth (contrasted to the slower, more erect growth of *C. rubella*). With toleration for lime but apparently rare on the more decidedly calcareous soils; its abundance on ravine-tops may be traced in part to the fact that all or most of the lime has been leached out of the soils there. It frequently is found on dry loamy banks with *Lophocolea minor* which is usually an indicator of at least subcalcareous conditions. Occasionally found on decaying logs with *Harpanthus, Nowellia,* and *Lophocolea heterophylla.*

The constant fertility and abundant, erect, often crowded perianths (frequently occurring 3-4 or more per plant) and the usually reddish-brown pigmentation (especially of the basal half of the perianth) characterize this species in the field. To be determined with certainty only with the microscope; here the absence of androecia on separate shoots as well as the fact that the bracts below the perichaetial ring are concave and distinctly larger

than normal leaves (Pl. 5, fig. 1), establish its paroecious nature. Except where very shaded, it constantly has the cell-walls of the leaves quite strongly thickened except occasionally on the protected, creeping sterile shoots (Pl. 5, fig. 3); this distinguishes it from our other paroecious species, *stellulifera* (differing also in having the cells over 16 μ long, and the leaves squarrose above). Confusion is perhaps most likely with *C. hampeana* which is often fully as fertile and frequently occurs under similar situations. *C. hampeana* however, always bears separate androecia on shoots arising from beneath the female shoot; frequently two or more androecia can be seen on a single shoot, the lower usually lacking antheridia; *hampeana* furthermore has the leaves of sterile shoots always with spreading-recurved or squarrose leaves and has the leaf-cells thin-walled. The generally larger (8-9 μ) spores and elaters also distinguish it from *rubella,* which has them rarely over 7.5 μ in diameter.

Douin has shown that most material formerly placed in *myriantha* is identical with *rubella.* Müller (1947a) and Buch (1936a) follow him in this and only Frye and Clark (1945) of recent workers, persist in using the name *myriantha.* The autoecious plant formerly called *rubella* is now considered either a pure synonym of *rubella* or separated out as the var. *bifida.* For this latter form Frye and Clark employ the name *rubella* contrary to modern usage, for instance that of Douin (1920) and that of Buch (1936a).

C. RUBELLA var. BIFIDA (Lindb.) Douin

C. rubella of Müller 1913, p. 153, of Macvicar, and of Frye and Clark.

Apparently quite rare: CHENANGO CO.: on rotten, peaty stump at edge of Plymouth Reservoir, *Schuster & Winne.*

The material listed above is doubtful. Critical examination indicates that the plants are autoecious, branches bearing separate androecia being present. This would exclude *C. rubella,* which otherwise agrees with the present species in most details — size of leaf-cells, and thickness of cell-walls, etc.

Associated species were *Tritomaria exsectiformis* and *Scapania irrigua.*

Douin has synonymized "*myriantha*" with *rubella.* Müller (1947a) follows him in this matter but Frye and clark (1945) still retain "*myriantha*" as a discrete species. Müller (1947a, p. 24) would go even further and considers *sullivantii* also a synonym of *rubella.* He clearly brings out the fact that Douin with his purely deductive approach, separated out as *sullivantii* all plants growing on decaying wood with a) ♀ bracts that were 3-lobed, b) underleaves on sterile shoots and c) perianth-mouth with cells 1.5-2 times as long as wide and more or less thin-walled. *C. rubella* was characterized as having a) ♀ bracts bilobed (thus with a 5-6 lobed involucre), b) underleaves of sterile shoots absent and c) perianth-mouth with cells about 3 times as long as wide and thick-walled. Müller clearly shows that Douin was separating individual plants of *rubella* as *sullivantii,* if they had the characters he assigned arbitrarily, to *sullivantii.* However Douin, oddly enough records *rubella* as constantly accompanying *sullivantii* but the fact escaped him that he was separating out individual extremes of the same species. Since Douin had made a new subgenus for *sullivantii (Dactylophyllum),* it apparently was impossible for him to comprehend the latter fact.

Müller, because of the variability of the *rubella-sullivantii* complex would consider the latter as a mere variety of *rubella*. Although for some time it was considered that *rubella* was autoecious and "*myriantha*" paroecious, there appears to be no specific value assignable to such differences in inflorescence. I therefore follow recent students in considering "*myriantha*" a synonym of *rubella* rather than Frye and Clark — the only recent workers who retain this artificial distinction.

However "*myriantha*" is commonly stated to have the leaf-lobes 4-5 cells broad, ovate-lanceolate, and on well-developed shoots sometimes with the lobes to 6-7 cells wide (especially on fertile shoots) while in *rubella* the lobes are narrowly triangular and only 3-4 (occasionally 5) cells wide at base. Whether this difference is based on genetic or environmental factors is not clear. Buch (1936a, p. 52) however, considers the nature of the inflorescence as of varietal importance, evidently following Douin. For the present I tentatively follow him in this. It has been clearly shown that almost all of the material previously called "*myriantha*" represents *rubella*. Frye and Clark do not accept this, hence their "*myriantha*" is the same as the *rubella* of modern European students and of this work. Buch (and Douin before him) separated out the autoecious form as the var. *bifida*. The name *bifida* was first used by Schreber in 1787, and was believed by Lindberg to be the same as *rubella* Nees; Douin however, stated this was highly uncertain. Later however, he used the combination *bifida* (Lindb.) Douin. It would seem best to drop the name *bifida* altogether, but if some agreement as to what name the autoecious plant shall bear will be arrived at, it will not matter essentially what name is retained. The present situation where *myriantha* is used by American workers for what is called *rubella* in European works and where *rubella* is used in America for *bifida*, is obviously appalling. All records of this complex cannot be accepted until some uniformity in usage is attained.

C. RUBELLA var. SULLIVANTII (Aust.) Müll.

Rare: TOMPKINS CO.: Coy Glen, 1944, *R. M. & O. M. Schuster*. CAYUGA CO: Paine's Creek near Aurora, 1945, *Schuster & Andrews*.

There is some doubt in my mind whether or not the above two collections refer to this form; the thinner cell-walls and small size however, are characteristic of this species rather than of *C. rubella*. Both collections as well as the other known collections of this northern form were from decaying, shaded, moist logs. Commonly associated forms are *Harpanthus scutatus*, *Chiloscyphus*, *Anastrophyllum hellerianus* and *Nowellia* as well as *Jamesoniella autumnalis*.

The minute size (usually less than 1.5 mm long), the usual presence of perianths which are not or scarcely contracted to the mouth, and the constant occurrence on moist decaying logs characterize this form. The small cells (mostly 10-12 μ) often with thin walls, separate it from our other paroecious species. Unfortunately, the cell size is scarcely different from some forms of *rubella*. The ♀ bracts are usually 3-lobed (resulting in an 8-9-lobed perichaetical ring), unlike in the closely related *rubella* (including *myriantha*).

Müller (1947a) takes Douin to task for creating a separate "subgenus" for this species and indicates it should be considered only a variety of *rubella*.

C. STELLULIFERA (Tayl.) Schiffn.

Rare. CATTARAUGUS Co.: no further data (*Hubert 71*) 1940; cited by Frye and Clark 1944, p. 530; collection examined by the writer. (Apparently the same collection cited by Boehner 1943, p. 12, from "base of tree at Nichol's Run, Limestone").

This species appears to be quite rare in North America; the present collection is the only definite citation of it from the United States I have been able to find. The very distinct appearance of the species makes misdetermination unlikely.

The squarrose leaves give this species the appearance of *C. hampeana* with which it agrees in the thin-walled cells. It differs from the latter in having much larger cells, as well as in the pareocious inflorescence. The squarrose leaves and large size of the cells also differentiate the species from our other two paroecious forms. This species usually has distinct, though small underleaves present except where destroyed below.

I have been able to study a small specimen of the above collection (through the courtesy of the Rev. P. Boehner). The plants, though sterile, can be almost certainly placed here. The large leaf-cells with very thin-walls (mostly 14-17 x 18-22 μ) and the yellow-green color of the plants are quite characteristic. Also rather typical is the tendency for the leaf-lobes or leaf-bases to bear occasional teeth. The latter is noted by Macvicar and is supposedly typical of many leaves occurring below the paroecious inflorescences.

The only species with which *stellulifera* could be confused is the European *C. baumgartneri* Schiffn., a calcicolous species also provided with large leaf-cells.

C. HAMPEANA (Nees) Schiffn.

Apparently common. TOMPKINS Co.: Enfield Glen, *Schuster;* Sixmile Creek, *R. M. & O. M. Schuster;* Slaterville Swamp, on rotten log, with *Nowellia* and *Jamesoniella, Schuster.* CHENANGO Co.: very decayed, moist wood, with *Tritomaria exsectiformis, Schuster & Winne.* ONTARIO Co.: Brigg's Gully, Richmond, *Schuster.* CATTARAUGUS Co.: Nichol's Run, Limestone; Martiny Rocks, West Branch of the Four Mile Road, Allegany; Pumpkin Hollow, Five Mile Road, Allegany (Boehner 1943, p. 12).

Occurring in some abundance on sandy-loamy, exposed soil under similar conditions as *C. rubella*; less frequently on rocks or ledges than *C. byssacea* but occasionally found intermingled with that species (Brigg's Gully) on sterile, rocky, open slopes, with such species as *Lophozia barbata, L. bicrenata* and *Ptilidium pulcherrimum.* At other times more moist soil over ledges, with *Scapania nemorosa,* etc.

Fruiting very freely and usually with perianths; the terminal (Pl. 4, fig. 9) or intercalary androecia often characteristically red-pigmented. The green or brownish-green rather than the reddish-brown color characteristic of *rubella,* the more flaccid stems, frequent occurrence under more mesophytic conditions than *rubella,* and the usually spreading to squarrose leaves of sterile shoots, separate this species from *rubella.* Under the microscope, the

broader leaf-lobes (generally 6-7 cells broad at base), the uniformly thin-walled cells, and the rather broad leaves (about twice as wide as the stem on sterile shoots) distinguish the species from *rubella*. Often it may be difficult to demonstrate the autoecious inflorescence since decay of the older parts of the plants makes it impossible to establish a clear connection between perianth- and androecia-bearing shoots. However, androecia and perianths always occur intermingled in the same mat. The species differs from the dioecious *byssacea* in lacking amphigastria on sterile shoots and in the virtually constant occurrence of inflorescences.

C. ELACHISTA (Jack) Schiffn.

Infrequent and local, but often overlooked. TOMPKINS CO.: McLean Bogs, *Schuster & Rader;* Woodwardia Bog, *Schuster & Rader;* Malloryville Bog, *Schuster & Rader;* Ringwood Swamp, on a decayed log lying in a shallow pool, *Schuster, Pendleton, Mathysse.* CHENANGO CO.: Plymouth Pond (Reservoir), S. Plymouth, on decayed peaty wood, with *Scapania paludicola, Cladopodiella,* etc., *Schuster & Winne.* SENECA CO.: Junius Sphagnum Bog, *Schuster.* CATTARAUGUS CO.: deep bog *Sphagnum,* Waterman Swamp, *Boehner* (det. by Schuster); swamp near Crystal Lake, with *Mylia,* Boehner (det. by Schuster).

A very characteristic member of the *Mylia* Associule of the open, sunny central portions of *Sphagnum* bogs, associated with *Cladopodiella, Cephalozia pleniceps* and *connivens, Calypogeia sphagnicola, Lophozia marchica,* etc. This is one of the few bog species that persists after the swamp loving ericaceous shrubs (*Ledum, Chameadaphne,* etc.) and finally trees have succeeded and covered the bog. Occasionally invading decayed logs lying in shallow ponds where *Sphagnum* is of localized occurrence (Ringwood), and occurring there with such species of decayed logs as *Cephalozia connivens, Lophozia porphyroleuca, Odontoschisma denudatum,* etc., but also with such bog forms as *Lophozia marchica, Sphagnum* and *Polytrichum* which locally may invade such logs lying in shallow ponds.

The bright to pale green color, alga-like appearance, very strongly spreading and distant leaves (divided about 4/5) with the lobes generally with 1-several sharp spinose teeth (Pl. 5, figs. 4-5), distinguish this species. The sharply spinose-dentate ♀ bracts with many of the marginal teeth recurved (Pl. 5, fig. 7) as well as the large leaf-cells with thin walls, are also diagnostic. The autoecious inflorescences are usually easily demonstrated.

Müller (1947a, p. 19) has gone into the question of the limits of this species. Douin (Bull. Soc. Bot. France 77: 196, 1930) had criticized the concept held by Jack (its author!), Gottsche, and Müller, as regards the identity of this species. He believed that these writers had *C. striatula* (=*subdentata*) before them. Müller in turn criticizes Douin's concept of the species and refutes his claims. Part of the controversy appears to originate in the fact that *elachista* usually has strongly recurved-spinose teeth on the margins of the ♀ bracts (Pl. 5, fig. 7) while *striatula* has smaller, mostly non-recurved serrations (Pl. 6, figs. 3, 6, 9-10). Müller (1912, p. 118) figured *C. elachista* on the basis of the original specimen, with non-recurved teeth on the margins of the bracts. Douin would call this *striatula.* He however, overlooks the fact that typical *striatula* may also have some of the teeth of

the bracts recurved and very prominent (Pl. 6, fig. 3, 6, etc.). He further overlooks the very significant fact that the species is typified by the type specimen and that, recurved marginal teeth or not, *elachista* must stand as delimited by Jack.

Müller (1947a, p. 21) also finds that in *elachista* the stem cells are about 16-20 x 40-55 μ (in *subdentata* only 9-12 x 20-25 μ) while the cells of the middle of the ♀ bracts are 20 x 50-65 μ in *elachista* (in *subdentata* only 10-13 x 18-30 μ). In spite of these additional differences that have been brought out, the two species remain extremely close and doubtfully specifically distinct as can be seen by the detailed analysis under *C. subdentata.*

Müller also, very justly criticizes the indefensible position taken by Douin who would derive *subdentata* from *byssacea,* i.e., an autoecious species from a dioecious, and *elachista* from *stellulifera.* Frye and Clark (1937-1947) go the latter even one better; they even separate the two species as "subgenera" (elevating the species groups of Douin).

C. SUBDENTATA Warnst. (=striatula Jensen)

Very rare in our region, previously unreported from the United States. GENESEE CO.: Bergen Swamp, May 1946, on hummocks of *Sphagnum* overlying the open marl bog, with *Microlepidozia setacea, Schuster et al.*

Critical students of the group like Müller, Macvicar, and Douin have retained "*striatula*" as a distinct species. In the key, eight or nine characteristics are given that typically serve to readily distinguish the two forms. However, most of these characteristics are merely the result of modification for a more xeric, exposed habitat frequented by the species, and perhaps also for a more cool climate. In North America, the two forms have a largely complementary distribution, "*striatula*" being the northern form, found from Greenland to Alaska and British Columbia, with the above the only locality south of that boreal and Arctic region. *C. elachista* proper, however, is found widely distributed throughout the Canadian and Transition Zones. The relationship of the two forms is somewhat parallel to that between the two species of *Ptilidium* except that the latter are more clearly differentiated and less variable.

In the material here placed under *subdentata,* the cells average less than 18 μ long and 10 μ wide, are (except in stems or sections of stems hidden among the *Microlepidozia,* and thus shaded) very thick-walled (Pl. 6, figs. 4, 8), with the wall 1/5-1/8 the width of the cells and in much of the material deeply reddish or reddish-purple pigmented; the cuticle of the leaves of all but strongly shaded material is strongly, prominently verrucose (Pl. 6, fig. 4); the stem has the epidermal cells very thick-walled (wall 1/4-1/6 as wide as cell) and the cells are relatively short (i.e., the stem-segments are short and the leaves therefore rather close, approximate except below); the leaves almost uniformly lack the 1- or more basal and sub-basal marginal spinose teeth characteristic of *elachista*; the bracteole and bracts are free or may be slightly united basally (Pl. 6, figs. 3, 5, 9-10); the perianth except at the hyaline mouth, is deeply purplish pigmented; the leaves are erect or

slightly erect-spreading, never spreading or squarrose. It follows from all of the above that the plant agrees decidedly more closely with *subdentata* than with typical *elachista*.

In the form of the perichaetial bracts the material from Bergen again agrees much more closely with *subdentata* than with *elachista*: the bracts on their apical halves are finely spinulose to spinulose-denticulate, partly merely serrate-dentate, and with relatively few of the recurved teeth characteristic of *elachista* (Pl. 6, fig. 3). In the single plant found with a mature capsule, the spores were reddish-brown, 8-12 μ in diameter (averaging about 11 μ) and were distinctly granular-punctate. They thus agree more closely with the dimensions generally given for those of *elachista* (in fact average larger than given in the descriptions of the various writers for *elachista*); the spore size however, does not impress me as very fundamental, especially since there appears to be considerable discrepancy in the size given by various writers in their color and in the form of their wall. Müller says the spores of *subdentata* are yellowish-brown, smooth and 6-8 μ in diameter (his description is copied, verbatim, by Frye and Clark); Macvicar states they are 7-8 μ, reddish-brown and granular-punctate; Meylan gives their size as 7-9 μ. There thus appears to be considerable variation in the form of the spores and it appears very doubtful whether size can be relied upon to afford any constant means of separation. This is indicated very strongly by the present plants which thus combine the characteristics of both *subdentata* and *elachista*. Critical study of the size of the spores, it is almost safe to predict, may show that the spore size will be found to become smaller with a decrease in length of growing season. Indeed, the converse certainly appears to hold and the distinctions between the two "species" appear to disappear when a Transition climate is reached. Subspecific treatment therefore appears to be indicated. However, the possibility cannot be dismissed that a mere extreme xerophytic modification *pachyderma-colorata-edentata-verrucosa* of *elachista* is at hand and approaches *subdentata* so closely that no differentiation can be made. The student will recall the work of Buch (1928) on *Scapania*, showed that leptodermous modifications of *S. irrigua* and *paludicola* could not be definitely separated from each other. Wherever the plant is placed, it is certain that the two forms are so closely related that specific treatment is stretching our concept of species. Most of the characteristics used in the key, represent tendencies rather than absolute differences and are therefore scarcely of specific value, even in the aggregate. Finally, study of shaded material associated with the more exposed specimens described above reveals some tendency towards intergradation with more typical *elachista*. Shaded material has relatively few or no verrucae on the cuticle and the cell-walls are notably thinner and approach typical *elachista*; the cell size increases somewhat in length, many cells being 18-24 μ long. The total lack of indication of sub-basal spinose teeth consisting of 1-3 cells differentiates the leaves of the leptodermous form *elachista*, however.

The form at hand differs from "typical" "*striatula*" in one regard: the lobes of the leaves average only about 3 cells wide at base, with probably more lobes 2 cells wide basally than 4 cells wide; no leaves were found at all

with the lobes 5 cells wide basally; in this it approaches *elachista*. Since the width of the leaf-lobes of the species of *Cephaloziella* varies very widely, depending on nutritional differences in the same species, too much significance cannot be attached to this difference.

In the writer's opinion it is exactly this immense variability of the species within a single clump only several centimeters square, that nearly precludes considering *subdentata* as a distinct species. A more considered opinion would be to consider the latter as no more than a subspecies of *elachista;* largely an ecological subspecies, partly a geographical subspecies, which has become constant enough to deserve a separate name, but which under some conditions may intergrade with *elachista* in nearly all of its characteristics. The extreme material studied from Bergen, with the cells guttulate, averaging about 10-12 x 12-14 μ, with the walls more than a fourth the width of the cells and with more or less distinct marginal, small teeth or crenulations, certainly appears specifically distinct (Pl. 6, fig. 8). The occurrence with it of specimens with thin cell-walls (less than 1/10 the width of the cell) and cells averaging 12-14 x 22-28 μ, and of all intergradations between the two, indicates that *subdentata* is merely a xerophytic extreme, replacing *elachista* almost entirely in the far north, which has, by virtue of its partial isolation, become moderately distinct from *elachista*. The occurrence of the form at Bergen Swamp is of some interest ecologically: the plant occurred, widely distributed, a few individuals at a time, on the high, relatively dry crests of the peat "hummocks" overlying open marl. Associated invariably was a decidedly pigmented form (mod. *colorata*) of *M. setacea* with quite closely imbricated leaves, occasionally *Mylia anomala, Cephalozia connivens, Odontoschisma denudatum,* and in one place, *Riccardia latifrons*. The plant occurred only on open hummocks where constant sun was the rule. It may therefore be questioned whether it may not represent merely a xerophytic modification of *elachista*, especially since the spore size agreed more with that of *elachista*. Such does not appear to be the case since one of the critical differentiating characteristics of *elachista* (presence of spinose basal teeth on some leaves) consistently failed to occur, and since even plants growing shaded by other plants (i.e., entirely green and with quite thin cell-walls) failed to show any indication of basal teeth. Such leptodermous modifications, though possessing a cell-net approaching *elachista* in size, still had the erect or erect-spreading leaves so characteristic of *subdentata*.

The position of Frye and Clark (1937-1947) who place *striatula* and *elachista* in separate subgenera on the basis of a slight difference in degree of coalescence of the bracts, does not appear tenable, especially since the material examined varies. Some bracts are entirely free from the bracteole, others very slightly connate at base with the bracteole (for about 0.1 its length) while in some perichaetial rings the bracteole is connate for nearly 0.2 its length with one bract and nearly free from the other bract (Pl. 6, figs. 3, 5, 9-10). According to their figures (chart, opposite p. 509) the bracteole is entirely free in *elachista* and connate with the bracts for 0.2-0.3 its length in *striatula*. The material here examined obviously bridges the gap between these figures and renders this distinction relatively valueless.

Family JUNGERMANNIACEAE

LOPHOZIA Dumort., s. lat.[20]

The Lophozioid complex is extraordinarily difficult as regards delimitation of genera. Correspondingly there has been a great deal of conflicting opinion as regards the number of genera and subgenera to be accepted in it. The older Scandinavian workers recognized but a single genus which they called *Jungermannia*. Boulay (Musc. de la France, 1904) also recognized a single genus, *Lophozia*. More recently, two genera, *Lophozia* and *Sphenolobus* have been recognized though the artificial character of the separation between them has been repeatedly emphasized (for instance by Müller and Macvicar). Still more recently, Buch (1933) divided the complex into some ten genera (*Lophozia, Orthocaulis, Anastrophyllum, Temnoma, Tritomaria, Saccobasis, Sphenolobus, Leiocolea, Barbilophozia, Isopaches*). These genera were accepted without question by Evans (1935). More recently some of them have been criticized by Meylan (1939) and Müller (1939). Buch (1941) also offered a modified scheme in which he recognized a lesser number of genera and more subgenera.

The underlying basis for Buch's approach however, has not been heretofore reevaluated or criticized. Buch divided the complex on the basis of stem structure, into two groups of genera, 1) *Sphenolobus, Anastrophyllum, Orthocaulis, Leicolea, Barbilophozia, Isopaches* (medulla of stem lacking a ventral small-celled band of cells that soon becomes infested by mycorrhizal fungi; the medulla essentially homogeneous); 2) *Lophozia, Tritomaria, Saccobasis* (stem differentiated into a dorsal region of large cells and a ventral medullary region of small, fungus-infested cells). The writer however, finds that this division into two basic developmental lines does not strictly hold. Therefore, even the less radical scheme given by Buch (1941) in which there is still some attempt made to maintain *Barbilophozia* and *Isopaches* as distinct from *Lophozia* (on the basis of a homogeneous medulla in the first two, a differentiated medulla in the latter) cannot be accepted in the light of more intensive study.

Firstly, in such species as *Barbilophozia hatcheri* and *barbata* there may be a slight indication of a ventral band (1-2 cells high) of smaller cells, indicating that the development of the ventral band is more a matter of degree than an absolute differentiating character. Secondly, in *Lophozia gracillima* supposedly with a ventral band, and in *Tritomaria quinquedentata* also supposedly with a large ventral small-celled region, the ventral "band" may be much more poorly developed than is true in *Lophozia silvicola* and *ventricosa*. In fact a series of drawings made haphazardly from a series of stems of

20 The classification of this complex is so subjective and so controversial that it is felt that much of the recent literature, either overlooked by Frye and Clark or issued since the appearance of their treatment (1945), should be reviewed and reevaluated, especially since the only recent review (Evans 1935) accepted, unquestioningly, the numerous genera established. Recent work, especially by Meylan, Müller, and the writer (only partly included here) definitely indicates that the existing systems of genera and subgenera (Buch 1933, 1941; Frye and Clark 1945) cannot be maintained without extensive modification.

different "genera" and species, will not allow a clear differentiation into two groups as Buch would have it. There is no clear breaking point i.e., no distinct difference in stem structure between the two types.

Of even more importance than the lack of a clear cut distinction in this regard (clear-cut distinctions, indeed cannot always be expected), is the fact that the stems of *Lophozia incisa, L. marchica* and *L. grandiretis*, three species placed without question within *Lophozia* by Buch both in 1933 and 1941, show absolutely no trace of a ventral band. They belong indubitably, in group 1 outlined above. (K. Müller 1939 on the basis of the oil-bodies separated these and related species as well as *L. obtusa* from *Lophozia* s. str. as the subgenus *Massula*). It would seem therefore, that at least a good share of the species placed into *Lophozia* until recently do not have the stem structure considered typical of *Lophozia* s. str. *(Dilophozia)*.

The writer therefore, believes that the concepts of relationships outlined by Buch as well as his generic entities, are not entirely valid. I would rather follow Müller (1939) who follows a much more conservative stand as regards generic lines in this complex and recognize a smaller number of genera.

Buch (1933) also erected the genus *Isopaches* to include two divergent elements: *Sphenolobus hellerianus* and *Lophozia bicrenata*. Meylan (1939) erected a new genus *(Crossocalyx)* for *hellerianus* and suggested that the other elements included by Buch in *Isopaches* be returned to *Lophozia*. Müller (1947a) would follow him in this. *Isopaches* was separated from *Lophozia* largely on the basis of a) the homogeneous medulla of the stem, and b) the fact that the cell-walls did not develop trigones but tended to become equally thickened.

I have pointed out that *Massula* also has a homogeneous medulla although no one has suggested that it does not belong in the genus *Lophozia*. Furthermore, *Massula* has a well-developed tendency to produce equally thick-walled leaf cells; this is especially marked in *L. (Massula) grandiretis*. Therefore, in the writer's opinion, there is not the slightest reason to exclude *Isopaches* generically from *Lophozia* on the basis of stem-structure (with the exception of the species *hellerianus*). In fact, *"Isopaches"* has the large and less numerous oil-bodies of *Lophozia* s. str. (subgenus *Dilophozia* of K. Müller) while it has the non-collenchymatous cells and homogeneous stem-medulla of *Massula*. Significantly, *"Isopaches" bicrenatus* has dentate ♀ bracts (characteristic of *Massula* but not of *Dilophozia*), and the paroecious inflorescence (common in *Massula* but nearly unknown in *Dilophozia*).

It seems therefore, that the "generic" characters of the groups previously placed in *Lophozia* s. str. are so closely interdigitated that a separation into well-defined genera is quite impossible. In the writer's opinion, the groups previously separated as genera are largely only of species-group or subgeneric standing. The question of the entire interrelationships of the Lophozioid complex will be taken up elsewhere in a more appropriate connection and critical fashion. For the present, I would recognize the following generic and subgeneric groups within the complex:

1. *Lophozia* Dumort.
   Subg. *Dilophozia* K. Müller
   Subg. *Isopaches* Buch
   Subg. *Massula* K. Müller
   Subg. *Barbilophozia* Lske.
   Subg. *Orthocaulis* Buch
   Subg. *Leiocolea* K. Müller

2. *Tritomaria* Schiffn.
   Subg. *Eutritomaria* subg. n.
   Subg. *Saccobasis* Buch

3. *Anatrophyllum* (Spruce) Steph.
   Subg. *Euanastrophyllum* subg. n.
   Subg. *Sphenolobus* (Lindb.) Steph.
   Subg. *Crossocalyx* Meylan

These groups can be separated very briefly by the following key which is given because of the unreliability of the key in Frye and Clark (1945, pp. 337-339) in which no attempt is made to key out groups in their entirety. In the general artificial key (pp. 518-523) no effort was made to key out these groups; they were all run out under "*Lophozia* s. lat." since it is virtually impossible to key out the genera and subgenera conveniently in an artificial key.[21]

KEY TO GENERA AND SUBGENERA OF THE LOPHOZIOID COMPLEX

1. Leaves with both dorsal and ventral halves of the insertion more or less oblique, usually quite distinctly so; frequently retaining underleaves (if leaves more than 2-lobed, medulla non-differentiated) 2
   2. Leaves all, or predominantly 3-4-lobed; medulla of stem uniform; perianth plicate; ventral leaf-margin often ciliate at base; underleaves normally retained and often large, ciliate 3
      3. Leaves predominantly 3-lobed, obliquely-subtransversely inserted ..... Subg. *Orthocaulis* Buch
      3. Leaves predominantly 4-lobed, very obliquely inserted and nearly horizontally spreading ..... Subg. *Barbilophozia* Lske.
   2. Leaves all, or predominantly 2-lobed; ventral leaf-margin never ciliate at base; if underleaves retained, the perianth is beaked at apex and not plicate 4
      4. Perianth terete, smooth, suddenly contracted at apex into a beak; underleaves usually retained; cuticle usually distinctly papillose or rugose-papillose; medulla of stem uniform; leaves nearly horizontally spreading, very obliquely inserted; oil-bodies 2-5 per cell, large (circa 5 x 10 μ) ..... Subg. *Leiocolea* K. Müller
      4. Perianth plicate, gradually contracted to the mouth, which is not beaked; underleaves totally absent; cuticle smooth;[22] leaves not horizontally spreading in a

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21 It is also so difficult to key out material to species (especially when sterile) on the basis of a key using characters leading to a differentiation of phyletically discrete groups, that I have not attempted to key out the species of this complex under their respective genera and subgenera but key them out under "*Lophozia* s. lat." (pp. 562-564).

22 Only in *Lophozia* (*Massula*) *obtusa* is the cuticle verruculose. Buch placed the species into *Leiocolea* in 1933. Müller (1939) on the basis of oil-bodies however, places it into his new subgenus *Massula*. Meylan (1939, p. 267) also criticizes the position given to the species by Buch and would place *obtusa* and *L. barbata* in close proximity. Müller (1939, p. 341) states that *obtusa* and *Leiocolea* have in common only the oblique leaf-insertion and nothing else. Meylan criticizes the disposition of *obtusa* in *Leiocolea* on the basis of the non-rostellate perianth mouth of *obtusa*. Buch (1941, p. 286-287) defends his viewpoint on the basis of the homogeneous medulla (which *Lophozia* is supposed not to show) which *obtusa* shows in common with *Leiocolea*.

It would seem to the writer that since he has been able to demonstrate that *Lophozia* (*sensu* Buch 1933, 1941) also may have a homogeneous medulla, the argument of Buch is not necessarily valid. The very minute, numerous oil-bodies of *obtusa* (versus the extremely large, few oil-bodies of *Leiocolea*) and the non-rostellate perianth mouth (distinctly beaked in *Leiocolea*), seem to be very basic reasons why *obtusa* cannot be placed in

nearly flat plane, somewhat obliquely inserted; oil-bodies smaller, 6-50 per cell, 2-9 μ long 5

5. Stem with medulla homogeneous, not forming a band of small ventral cells; female bracts more or less sharply dentate; cells not collenchymatous: the walls becoming equally thickened; often paroecious 6

6. Oil-bodies numerous, mostly 30-50 per cell, only 2-4 μ; cells larger, 28-36 μ to 50-60 μ; leaves often largely 3-lobed .....Subg. *Massula* K. Müller

6. Oil-bodies few, 6-18 per cell, 5-6 μ; cells smaller, always thick-walled and guttulate, 23-28 μ; leaves always bilobed ....Subg. *Isopaches* (Buch) emended Schuster

5. Stem with medulla dorsiventrally differentiated: above of large cells, below of small, shorter cells soon destroyed by mycorrhiza; female bracts with lobes non-dentate; cells always collenchymatous: the corners with distinct trigones, the walls always thin; never paroecious; oil-bodies 6-18 per cell, 4-9 μ long; leaves normally bilobed .....Subg. *Dilophozia* K. Müll.

1. Leaves with at least dorsal half of insertion transverse, or directed to stem-apex, the ventral half oblique to subtransverse: the leaves appearing distinctly transversely inserted, with the leaf-plane at right angles to the stem-axis or nearly, the leaf-lobes often loosely folded over each other and complanate; underleaves always totally lacking; leaves 2-3-lobed (if 3-lobed, the medulla with a ventral band of small cells) 7

7. Stem with a distinct dorsiventral differentiation of the medulla: the ventral region of much smaller, shorter cells; leaves predominantly 3-lobed; dorsal leaf-insertion not decurrent. *Tritomaria* Schiffn. 8

8. Leaves unequally 3-lobed usually (equally in *scitula*); cortical stem-cells with walls much thinner than width of lumen; dorsal half of leaf-insertion simply transverse .....Subg. *Eutritomaria* subg. n.

8. Leaves shallowly equally trilobed; cortical stem-cells with walls as thick as width of lumen; dorsal half of leaf-insertion curved towards anterior end of stem .....Subg. *Saccobasis* Buch

7. Stem with no distinct dorsiventral differentiation of the medulla; leaves all 2-lobed. *Anastrophyllum* (Spr.) St. 9

9. Leaves with dorsal half of insertion transverse, non-decurrent; female bracts more or less sheathing perianth, often dentate; leaves widest near middle, oval in shape or oval-rectangular 10

10. Stem only 6-7 cells thick; seta of 4 inner, 8 rows of outer cells; gemmae at apices of slightly of moderately modified shoots ....Subg. *Sphenolobus* (Ldb.) St.

10. Stem only 6-7 cells thick: seta of 4 inner, 8 rows of outer cells; gemmae at apices of flagelliform, slender shoots .....Subg. *Crossocalyx* Meylan

9. Leaves with basal part of dorsal insertion transverse, then swiftly decurrent, the basal part of the leaf extending across the stem; bracts spreading from perianth, entire-margined; leaves widest basally .....Subg. *Euanastrophyllum* subg. n.

Leiocolea. Since I am able to show that the stem structure of *Massula* agrees with both that of *Leiocolea* and *obtusa*, the stem structure no longer is a criterion that can be used in indicating in which of the two groups *obtusa* should be placed. Since the other characters agree better with *Massula*, I follow Müller in his disposition of the species, tentatively.

It must be stressed however, that the striate-verruculose cuticle of *L. obtusa* is closer to that of *Leiocolea* than to the smooth cuticle uniformly occurring in *Massula*. This might indicate that the disposition of *obtusa* as a subgenus (*Obtusifolium*) as done by Buch (1941, p. 289) may be warranted. For the present little is to be gained by establishing a new subgenus on the basis of a slight difference in cuticle.

ARTIFICIAL KEY TO SPECIES OF LOPHOZIA, S. LAT.

1. Leaves all or mostly 3-4 lobed on normal sterile shoots (Pl. 7, figs. 1, 2, 8, 11; Pl. 9, figs. 4, 6); underleaves absent or minute on sterile shoots 2

2. Leaves decidedly asymmetrical, widest near base, (the third, anterior lobe appearing as a mere sharp tooth; the two ventral lobes approximate, often combined on gemmae-bearing shoots) (Pl. 9, figs. 4, 6); leaves transverse; always with reddish-brown gemmae at apices of shoots; stem in cross-section with small ventral medullary cells. *Tritomaria* 3

3. Gemmae elliptical, smooth (Pl. 9, fig. 5), 14-19 x 9-12 μ; cells of leaf-middle 14-20 μ long, of antical margin 14-15 μ ..... *Tritomaria exsecta*

3. Gemmae angular or pyriform (Pl. 9, fig. 7), 18-25 x 14-18 μ; cells of leaf-middle 26-42 μ long, of margins about 20 μ ..... *Tritomaria exsectiformis*

2. Leaves nearly symmetrical, widest on apical third, the lobes subequal (Pl. 7, figs. 1-2, 8, 11; Pl. 9, fig. 1); leaves more or less distinctly succubous, obliquely inserted; cross-section of stem with the medullary cells uniformly large. *Lophozia*, in part 4

4. Leaves nearly transverse, acutely 3-lobed (Pl. 7, fig. 11); erect, attenuate shoots bearing appressed reduced leaves and gemmae common (Pl. 7, figs. 8-10) ..... *L.* (*Orthocaulis*) *gracilis*

4. Leaves very succubously and obliquely inserted (Pl. 7, fig. 1); erect gemmiparous shoots bearing gemmae absent 5

5. Leaves normally 4-lobed (Pl. 7, fig. 2), densely chlorophyllose, dark green to brownish, not wavy and undulate; cells less than 25 μ; not in bogs ..... *L.* (*Barbilophozia*) *barbata*

5. Leaves very irregular: many 2-lobed, some 3-4-lobed, wavy and undulate, rather transparent (Pl. 9, fig. 1), pale green or reddish-tinged; cells over 35 μ; in swamps or bogs 11

1. Leaves all 2-lobed (very occasionally with isolated leaves 3-lobed), the two lobes subequal (Pl. 7, figs. 5, 7, 14, 16; Pl. 8, figs. 2, 7); in one species the lobes bearing 1-several spinose teeth on some leaves; in several species the gemmiparous leaves becoming irregularly dentate 6

6. Leaves transverse or nearly, more or less concave or concave-canaliculate (Pl. 7, figs. 5, 16; Pl. 9, fig. 8), at least the dorsal half of the insertion transverse; cell-walls thickened, often yellowish, the cells of leaf-middle 18-24 μ or less (Pl. 7, figs. 12-13; Pl. 9, fig. 10); amphigastria absent; gemmae reddish or purple; medulla undifferentiated. *Anastrophyllum* 7

7. Minute species, less than 0.5 mm wide x 0.8 mm long; gemmae 1-celled, quadrate, vineous red, 10-12 μ (Pl. 7, fig. 6), at tips of erect, filiform shoots with appressed leaves (Pl. 7, fig. 4); only on decaying wood ..... *A.* (*Crossocalyx*) *hellerianus*

7. Larger species, 0.8-3 mm wide x 1-5 cm long; gemmae 15-30 μ long, largely 2-celled, at apices of shoots not sharply differentiated from gemmae-free shoots (Pl. 7, fig. 15); rarely on decaying wood; stem 10-15 cells high in cross-section 8

8. Leaves regularly, pectinately inserted, the dorsal half of the insertion not at all decurrent (Pl. 9, fig. 8), the leaves not widest basally, distinctly canaliculate; dorsal lobe lying loosely applied over ventral lobe; cells equally thick-walled (Pl. 9, fig. 10); bracts sheathing the deeply plicate perianth; gemmae scarlet to carmine; plant 0.8-1.2 mm wide, very slender ..... *A.* (*Sphenolobus*) *minutus*

8. Leaves not stiffly, pectinately inserted, the dorsal half of the insertion distinctly decurrent (Pl. 7, figs. 14, 16), the leaves widest near base, not canaliculate; dorsal lobe spreading and erect; cells with bulging yellow trigones

(Pl. 7, figs. 12-13); bracts spreading away from the largely smooth perianth (Pl. 7, fig. 16); gemmae purplish-black when in masses ..... *A.* (*Euanastrophyllum*) *michauxii*

6. Leaves strongly succubously inserted: both dorsal and ventral halves of the insertion oblique (Pl. 8, figs. 7, 17; Pl. 9, figs. 1, 3), usually more or less horizontally spreading (at least the lower leaves); cells of leaf-middle 25-50 μ, with the walls usually thin (Pl. 8, figs. 1, 6, 13), thick in only one species. Lophozia, in part 9

9. Underleaves very large, obvious, deeply divided and ciliate-laciniate; cells 35-48 μ, with bulging trigones and coarsely verruculose cuticle; leaves widest near base, wider there than long, horizontally spreading; gemmae absent ..... *L.* (*Leiocolea*) *rutheana*

9. Underleaves absent or vestigial, linear or lanceolate when present (never half as long as a leaf); cuticle nearly or quite smooth; cells less than 35 μ (or walls thin, lacking trigones, and with gemmae) 10

10. Cells thick-walled and guttulate (Pl. 8, fig. 14), 23-28 μ; gemmae abundant, reddish-yellow, on shoots with more or less dentate leaves; paroecious: the bracts and leaves below them dentate (Pl. 8, fig. 17); leaves as wide or wider than long, orbicular; stem with uniform medulla ..... *L.* (*Isopaches*) *bicrenatus*

10. Cells not with uniformly thick walls (Pl. 8, figs. 6, 1); if stem with uniform medulla, the gemmae not reddish-yellow 11

11. Cells thin-walled, large, mostly 36-48 μ; leaves undulate and wavy, hyaline, very irregular, more or less distant, some always 3-4 lobed (Pl. 9, fig. 1); gemmae ovoid, greenish; only in bogs and swamps; medulla of stem of uniform, large cells 12

12. Stem purplish below, the rest of the plant uniformly green; cells many over 45 μ; only in Sphagnum bogs ..... *L.* (*Massula*) *marchica*

12. Stem and rhizoids not purplish tinged, but the entire plants and perianths often reddish; cells many 35-40 μ ..... *L.* (*Massula*) *mildeana*

11. Cells smaller, 23-36 μ long; leaves approximate to imbricate, regular, usually all 2-lobed (or irregularly dentate); gemmae entirely angular, greenish or purplish or reddish-yellow (Pl. 8, figs. 5, 12); on decaying wood, rocks, or soil 13

13. Paroecious, the leaves below the perianth concave, more or less dentate-margined (Pl. 8, fig. 4); involucral bracts finely dentate; leaves orbicular, as wide or wider than long; gemmae purplish; cells thin-walled, 28-38 μ (Pl. 8, fig. 6) ..... *L.* (*Dilophozia*) *excisa*

13. Dioecious; gemmae greenish, reddish-yellow, or absent; involucral bracts normally not dentate 14

14. Plant opaque bluish-green, densely chlorophyllose, to 1 cm long; stem thick and fleshy, the leaves crowded distally at least and usually forming a crispate "head"; leaves divided into 2-3 acute to acuminate lobes, which may again bear 1-several teeth (Pl. 8, fig. 11); gemmae yellowish-green; medulla of stem uniform ..... *L.* (*Massula*) *incisa*

14. Plant never opaque bluish-green; stem slender, the leaves never crowded, not forming a crispate head; leaves with broad acute to obtuse lobes that are free of teeth 15

15. Gemmae usually present (if absent, trigones bulging) (Pl. 8, fig. 8); cells 24-30 μ, usually with small to distinct trigones (Pl. 8, fig. 1); stems opaque; perianth usually present, distinctly plicate and never beaked (Pl. 8, fig. 2); underleaves quite lacking; cuticle always smooth; stem with medulla dorsiventrally differentiated 16

16. Leaves squarrose below, erect-spreading above (Pl. 8, fig. 7), longer than wide, the lobes often rather drawn out (Pl. 8, fig. 9); trigones small; gemmae reddish-yellow; perianth-mouth ciliate-dentate. (Upper leaves of erect or ascending gemmiparous shoots with nearly transverse, characteristically erect-spreading leaves) ..... *L. (Dilophozia) longidens*

16. Leaves never squarrose, as wide as long, the lobes not slender and drawn out (Pl. 8, figs. 2, 10); gemmae greenish-yellow or absent; upper leaves of gemmiparous shoot obliquely inserted and spreading like lower leaves, the gemmiparous shoots rarely strongly ascending. (If perianth mouth ciliate-dentate, the trigones bulging) 17*

17. Trigones large, bulging (Pl. 8, fig. 1); perianth mouth ciliate-dentate with teeth mostly 3-5 cells long; usually more or less reddish tinged; only on organic substrata; leaves only 0.7-0.9 as wide as long ..... *L. (Dilophozia) porphyroleuca*

17. Trigones usually small or nearly absent (as in Pl. 8, fig. 6); perianth mouth crenulate-dentate with teeth 1-2 cells long; usually green throughout; leaves mostly 0.95-1.1 as wide as long (Pl. 8, fig. 10); on rocks and as a chasmophyte ..... *L. (Dilophozia) ventricosa*

15. Gemmae constantly absent; cells 26-35 μ (Pl. 9, fig. 2); perianth smooth, terete, suddenly contracted to a short beak (Pl. 9, fig. 3); underleaves present if plant more than 12 mm long; cuticle often verrucose; stem with medulla of uniform, large cells 18

18. Plant small, 8-12 mm long; cells 30-35 μ, with small trigones (Pl. 9, fig. 2); underleaves entirely absent ..... *L. (Leiocolea) badensis*

18. Plant larger, 1-3 cm long; cells 26-32 μ, usually with large trigones; underleaves present but small ..... *L. (Leiocolea) muelleri*

I. LOPHOZIA Dumort. s. str.

Subgenus ORTHOCAULIS Buch

L. (ORTHOCAULIS) GRACILIS (Schleich.) Steph. (ATTENUATA Mart.)

Very rare. CATTARAUGUS CO.: about one mile north of Rock City, 1945, *Schuster & Rader;* on conglomerate rocks at top of Martiny Rocks, West Branch of the Four Mile Road, Allegany, at an elevation over 2000 feet (Boehner 1943, p. 13); Waterman Swamp, Napoli, with *Bazzania trilobata,* on rotten wood and soil, *Boehner* (det. by Schuster). ONONDAGA CO.: Jamesville Road (Goodrich 1912, p. 22, 1912).

The present species is decidedly northern, occurring from the Arctic-alpine into the Canadian Zone; it is furthermore a montane and submontane species being absent in the lowlands except in the far north. For these reasons, the Onondaga County record needs corroboration; I have been unable to locate an authentic specimen of the species from there. The "calciphobous" nature of the species would make its occurrence there seem very unlikely unless it was found on decaying wood.

The records of the species from Cattaraugus County are based on specimens collected on quartz conglomerate, growing associated with *Jamesoniella*

* See Appendix, p. 703, for *L. alpestris.*

autumnalis, Bazzania trilobata and *Cephaloziella byssacea* at an elevation of about 2400 feet. Other Canadian species such as *Tritomaria exsecta* and *exsectiformis, Bazzania denudata, Anastrophyllum minutus* and *michauxii* occurred under similar but more moist conditions. The local distribution indicates the species is a relict form here, known again from a single record from Pennsylvania and one from Tennessee to our south; its rarity or absence throughout nearly all our area is apparently due to the lack of siliceous rocks elsewhere, and to the relatively lower elevations. (Pl. 7, figs. 8-11).

Subgenus BARBILOPHOZIA Loeske

L. (BARBILOPHOZIA) BARBATA (Schmid.) Dumort.*

Rare locally. TOMPKINS CO.: Coy Glen, 1893, *Durand;* Sixmile Creek, 1945, *R. M. & O. M. Schuster.* YATES CO.: moist bank north of Middlesex, *Schuster & Pendleton.* ONONDAGA CO.: Primrose Hill (Goodrich 1912, p. 22). CHEMUNG CO.: Veteran, near Elmira, *Schuster, Rader, Smith.* ONTARIO CO.: Briggs Gully, Richmond, *Schuster.* STEUBEN CO.: moist ledges near Woodhull, 1945, *Schuster & Rader.* CATTARAUGUS CO.: Pumpkin Hollow, Five Mile Road, and Martiny Rocks, Four Mile Road, Allegany (Boehner 1943, p. 13).

Our only species of *Barbilophozia* that occurs south of the "Hudsonian" zone; the species is everywhere local and apparently fairly rare throughout central and western New York. In general it is rare south of the Canadian zone, and away from the montane and submontane areas of New England, and northern New York. It has a rather moderate toleration for lime, occurring very frequently with the calciphilous *Lophocolea minor* but mostly absent from decidedly calcareous areas. Frequently on either the northern or southern slopes or crests of ravines occurring with *Lophozia bicrenata, Cephaloziella hampeana, byssacea,* more rarely with *Lophozia incisa* and *excisa.* Limited in occurrence to the thin, stony, loamy or sandy-loamy soils or to the rock-outcrops where these generally occur; able to tolerate much direct sunlight and usually a decided xerophyte. The more widespread occurrence in siliceous regions indicates that the tolerance for lime is not very great, hence acts as a limiting factor locally. As can be gathered from the above, generally a member of the *Lophozia bicrenata-Cephaloziella* Associule but occurring most often with the *Lophocolea minor* facies. At the Steuben County locality, it grew directly on sheltered shale outcrops associated with such species as *Scapania nemorosa, S. mucronata,* etc., and *Lophozia excisa* where it invaded soil, here again occurring in a *Lophocolea minor* facies of the *Scapania* Associule.

Our only species with succubous, mostly 4-lobed leaves (Pl. 7, figs. 1-2). Poorly developed material frequently has only 2-3 lobed leaves but some stems always occur that show the 4-lobed condition.

Subgenus LEIOCOLEA K. Müll.

L. (LEIOCOLEA) BADENSIS (Gottsche) Schiffn.*

Frequent, but very local. TOMPKINS CO.: Taughannock Gorge, *Andrews, Schuster;* Buttermilk Glen, *Andrews, Schuster;* Lick Brook, *R. M. & O. M. Schuster;* Sixmile Creek, *Andrews, Schuster;* Coy Glen, *Andrews, Schuster;* Enfield Glen, *Andrews, Schuster;* Fall

* See Appendix, p. 703.

Creek Ravine, *Schuster*. CAYUGA CO.: Paines Creek near Aurora, Oct. 15, 1945, in fruit, *Schuster & Andrews*.

This species probably occurs on many of our moist, somewhat sheltered, vertical, calcareous ledges; probably to be found in every large ravine where moist, calcareous out-crops occur. Associated almost invariably with *Gymnostomum curvirostre*, very often with *Preissia quadrata, Pellia fabbroniana, Conocephalum* and *Riccardia pinguis*, occasionally with *Scapania mucronata*, always on ledges in the Pine-Hemlock-Yellow Birch Ravine subclimax. Occurring under conditions of somewhat greater exposure and more decidedly mesophytic or meso-hygrophytic than *Reboulia*, hence a characteristic member of the *Preissia-Riccardia pinguis* Associule. Unlike most of the members of that Associule, the present species appears to be limited to cliffs and ledges, or thin soil in crevices or at their crests.

Its frequency locally is to be traced directly to the widespread calcareous conditions that occur.

When sterile, distinguished with difficulty; in the above key I have indicated where it would key out on the basis of sterile material. When fertile, the terete, smooth perianths, suddenly contracted to a beaked apex (but not set in a depression as in *J. lanceolata*) are absolutely characteristic (Pl. 9, fig. 3); they are fortunately usually present. The absence of gemmae and the thin-walled, large cells (Pl. 9, fig. 2) help to distinguish it when sterile from our other *Lophoziae;* the total lack of amphigastria will distinguish it from other related forms with bilobed leaves.

Macvicar (1926) gives the "fruiting"-time as April-June; I have found it with mature capsules as late as October, indicating a tendency to produce mature sporophytes late in the fall.

Previously reported from "Ithaca" (Evans).

L. (LEIOCOLEA) MUELLERI (Nees) Dumort.

Very rare. CATTARAUGUS CO.: "Found on the campus of St. Bonaventure College (St. Bonaventure, N. Y.), growing on soil" (Boehner 1943, p. 13); not seen by the writer.

A decidedly "calciphilous" species like the closely related *L. badensis*. I have not found this species in our region and wonder if the material could possibly be the latter species.

The terete, smooth perianths, suddenly contracted into a short beak, separate this species from all other of our Hepaticae with bilobed leaves except *L. badensis* and *rutheana*. The presence of small, subulate to lanceolate, entire, or laterally slightly dentate amphigastria, the slightly smaller leaf-cells (averaging less than 32 μ in the leaf-middle), the rather more apiculate leaf-lobes generally ending in two single cells, and the larger size (2-3 cm long, rather than 8-12 mm long), separates *L. muelleri* from *badensis*. The much smaller leaf-cells and the minute size of the amphigastria as well as the dioecious inflorescence separate *muelleri* from *rutheana*.

Sterile material of all three of these species can be separated from other

bilobed-leaved species by the very large, somewhat grayish oil-bodies (usually 5 x 9 μ or even larger) which occur mostly 2-3 per cell. All three of our species further differ from other Lophozioid species in never producing gemmae and in the homogeneous stem-medulla.

L. (LEIOCOLEA) RUTHEANA (Limpr.) Howe

Extremely rare and local. GENESEE CO.: Bergen Swamp, among calciphilous mosses and *Moerkia, Riccardia pinguis, R. multifida,* directly over wet marl, May 1946, *Schuster & Winne.* Not previously reported east of Michigan.

The occurrence of this species in New York is truly remarkable. The previous records establish the species in northern Michigan, Yukon Territory and in northeastern Minnesota but nowhere else in the New World.[23] The species is essentially circumboreal in distribution but is very rare in the lower portion of the Coniferous Panclimax while it has been entirely unknown from the Deciduous Panclimax area. Müller (1905-1916, p. 715) comments on the fact that the southernmost peripheral points in the distribution of the species all lie within the edge of the glaciated area in Europe. The North American distribution appears to fall within the same pattern.

Like other members of the subgenus *Leiocolea, L. rutheana* is a pronounced "calciphile" which occurs under mesic or mesic-hygric conditions and has a zonal distribution ranging from the *Chameadaphne* Heath Associes to the *Thuya* Forest Associes. The species is virtually restricted in occurrence to marl bogs (unlike our other two *Leiocoleas*).

The species can scarcely be confused with any other local species. The large size (3.5-8 cm long), the decidedly aromatic odor when fresh, and the broad, bilobed leaves with a distinctly decurrent postical base, separate it in the field. Under the microscope, the very large underleaves (similar to Pl. 7, fig. 3 in form), a few of which may be half as long as leaves,[24] and the large cells (with the median ones 35-48 μ long or more x 32-40 μ wide) with thin walls but bulging trigones are diagnostic.[25]

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23 The occurrence of such a decidedly "western" species in Bergen Swamp is not without precedent. The occurrence of *Cypripedium candidum, Zygadenus chloranthus, Juniperus horizontalis* in the same area is highly significant.

24 Frye and Clark (p. 380) separate *rutheana* on the basis of size of underleaves. This appears an unfortunate characteristic to use since few of the underleaves are "more than half as long as the leaves."

25 According to Frye and Clark *rutheana* may be separated from *harpanthoides* because it has "colorless" cell-walls. In the material at hand the cell-walls are decidedly golden brown and so deeply pigmented that the entire plant may acquire a brownish-green color as a result. According to the keys of Frye and Clark therefore, the species would be sought under *harpanthoides.* This appears to be an unfortunate selection of key characters which again is used to separate *Sphenolobus* from *Anastrophyllum,* without any more validity. Since such pigmentation of the cell-walls is directly correlated to illumination, the use of such environmentally controlled characteristics as key characters should be avoided. None of the European specialists have attempted to utilize such superficial characters for diagnostic purposes.

Subgenus DILOPHOZIA K. Müll.

L. (DILOPHOZIA) LONGIDENS (Lindb.) Macoun

Very rare, apparently a relic species locally. CATTARAUGUS CO.: "on soil along South Branch of Cattaraugus Creek, Gowanda" (Boehner 1943, p. 12); not seen by the writer.

This is essentially a species of the subarctic-subalpine Coniferous Zone (Canadian-Hudsonian of Merriam). It is extremely limited in occurrence in the region to the south of that zone. The species has a wide tolerance further northward; occurring on rotting logs as well as on soil, as a chasmophyte on cliffs, or as a primary invader on sheltered ledges and cliffs.

This distinctive species need not be confused with any other local form. The relatively narrowly ovate-rectangular leaves (Pl. 8, fig. 9), which are inserted nearly transversely on the erect or strongly ascending stems (Pl. 8, fig. 7 are quite characteristic). This is our only local species of *Dilophozia* (if Müller's name is to be used) that has a well-defined tendency to grow suberect under the most diverse conditions. The conspicuous masses of reddish-yellow gemmae are also quite characteristic (Pl. 8, figs. 7, 8). Frye and Clark (1945, p. 364) describe them as "yellowish-brown to reddish brown or green" in spite of the fact that Buch (1933) clearly showed that the species never, even under extremely diffuse illumination, develops greenish gemmae. This leaves one wondering whether Frye and Clark confused *gracillima* Buch, a species with green gemmae, with *longidens*. They obviously do not consider *gracillima* as a synonym of *longidens* since they do not refer to it in their work. It seems necessary therefore, to call attention to the fact that *longidens* always has reddish-yellow gemmae, especially so since the writer has recently discovered *gracillima* in the United States (Minnesota and Michigan).

L. (DILOPHOZIA) VENTRICOSA (Dicks.) Dumort.*

Scarce locally. TOMPKINS CO.: Fall Creek Ravine, at crest, on thin soil and in crevices of rocks, *R. M. & O. M. Schuster;* Enfield Glen, in crevices of moist shale, *R. M. & O. M. Schuster;* Lick Brook, on thin soil on shale that is seasonally moist, near ravine crest, *R. M. & O. M. Schuster.* ONONDAGA CO.: "Clay" (Goodrich 1912, p. 22). ONTARIO CO.: Briggs Gully, *R. M. Schuster.* STEUBEN CO.: north-facing ledges, on thin, shaded soil, east of Woodhull, *R. M. Schuster & W. Rader.*

Locally, apparently confined to near the crests of ravines and ledges where it grows on thin soil over rocks or in crevices of the rock, i.e., typically a chasmophyte; often only occurring in very small quantity and not well developed. Associated are *Cephaloziella hampeana, Scapania nemorosa, S. mucronata, Diplophyllum apiculatum,* and almost always, *Tritomaria exsectiformis* as well as, rarely *Lophozia barbata.* Local distribution indicates the species has a slight toleration for lime unlike the closely related *L. porphyroleuca.*

The normally green color and the almost constant occurrence of yellow-green gemmae-masses on the tips of the bilobed leaves, *even on leaves halfway down the stem,* alone are sufficient to characterize the species locally. Locally this species has the leaves mostly between 0.85-0.95, rarely 1.05 as wide as long. The collections are all from relatively little exposed and only

* See Appendix, p. 703.

moderately insulated areas. Therefore it may be questioned whether the local material should not be referred to the questionable species *L. silvicola* Buch. The latter even under exposed conditions, has the leaves merely 0.75-0.95 as wide as long (as in *porphyroleuca*) and always has from 15-25 oil-bodies per leaf-cell. This is somewhat higher than in *ventricosa* where the maximum is from 12-15 per cell. Furthermore, *silvicola* has the oil-bodies with a small-to-large central oil-globule, more highly refractive than the "mantle" of obscure, smaller oil-globules surrounding it. In *ventricosa* on the other hand, the oil-bodies are uniform throughout, consisting of numerous small, obscure oil-globules, giving the entire oil-body a somewhat vesicular to granulose appearance. Müller (1939) has suggested that *silvicola* is a synonym of *ventricosa* but the limited experience the writer has had with *silvicola* suggests that it is a distinct genotype form rather than a modification. Whether any of the local material should be referred to *silvicola* must await collection of living material. Since shade forms of *ventricosa* may have the leaves narrower than long (as is typical of all *silvicola*) the leaf-form of the local material cannot be used in arriving at a decision.

Both *ventricosa* and *silvicola* agree in the form of the perianth-mouth; this is provided with fine teeth merely 1-2 cells long. This contrasts with the perianth-mouth of the next species (*porphyroleuca*) in which many of the teeth of the perianth-mouth are 3-4 cells long.

L. (LOPHOZIA) PORPHYROLEUCA (Nees) Schiffn.

Rare locally. TOMPKINS CO.: Ringwood Swamp, fruiting abundantly April 19, 1945, *Schuster;* Freeville Swamp. GENESEE CO.: Bergen Swamp, with mature capsules April 28, 1945, *R .M. & O. M. Schuster.* CHENANGO CO.: Plymouth Pond, near S. Plymouth, *Schuster & Winne,* with *Scapania irrigua* and *paludicola,* etc. ONONDAGA CO.: "near Syracuse" (Underwood & Cook, Hep. Amer. No. 112, as "*Jungermannia excisa*); Jamesville, *Underwood & Cook,* as "*L. guttulata.*"

Occurring always on decaying, rather moist, deciduous-tree logs, a typical member of the *Odontoschisma-Jamesoniella* Associule of wet rotten wood, usually occurring in rather exposed places at the edges of swamps; actually able to tolerate much direct sunlight and then usually deeply reddish-pigmented. *Nowellia curvifolia* is commonly found on the vertical, more shaded sides of the logs and generally associated with *Cephalozia connivens, Riccardia latifrons* and other shade-loving hygrophytic humicolous and xylicolous species.

The constant occurrence locally, on sunny, decaying logs, as well as the large, bulging trigones (Pl. 8, fig. 1), and the ciliate perianth mouth (with the teeth mostly 2-5 cells long) (Pl. 8, fig. 2), easily differentiate this species, when typical. None of the material I have seen locally bears gemmae and therefore belongs to the "*guttulata*" modification. Buch (1933a) has shown that this species may be virtually inseparable from *ventricosa* which may also develop bulging trigones under extreme conditions. The present species however, has the leaves always slightly narrower than long (about 0.75-0.95 as wide as long) and is usually rather strongly reddish-tinged when exposed (although *ventricosa* may also show reddish pigmentation). Buch has shown

* See Appendix, p. 703.

by culture experiments that *porphyroleuca* is a genetically discrete form though it may produce modifications with small trigones that are inseparable from *ventricosa.*

L. (DILOPHOZIA?) EXCISA (Dicks.) Dumort.*

Apparently rare locally. STEUBEN CO.: on thin, sandy-loamy, moist soil over north facing shale ledges, east of Woodhull, *Schuster & Rader.* CATTARAUGUS CO.: "Collected in the county at various stations" (Boehner 1943, p. 12). (The species has also been reported from Onondaga County, by Goodrich 1912, p. 22, from "East Syracuse"; this report is extremely doubtful and may refer to the report of the species from "Syracuse" [Underwood & Cook, 1891, Hep. Amer. No. 112, labelled "*Jungermannia excisa*"]. I have examined a specimen of the latter number which was taken from "stumps"; it contains *Lophozia porphyroleuca, L. incisa, Jamesoniella autumnalis* and *Blepharostoma trichophyllum.* Frye and Clark (1945, p. 348) also cite this number under their "Examinations" from Syracuse; they however can scarcely have critically studied the specimen since *L. excisa* differs in several fundamental characters from *porphyroleuca. L. excisa* furthermore, appears to be able to invade inorganic substrates only and rarely or never occurs on decaying logs or stumps. It is apparent therefore that Goodrich and Frye and Clark simply are perpetuating the earlier error of Underwood and Cook and that their reports do not represent new collections. The collections by Boehner also need re-examination since in the writer's experience *L. excisa* is quite rare locally and has been largely confused with the superficially similar *L. bicrenata.*)

This again is an essentially Hudsonian-Canadian Zone species rare in the Transition Zone, and probably occurring within it only as a disjunct and relic of glacial times. The records from Connecticut and Tennessee are our only other southern records. Locally the species was associated with *Scapania mucronata, Lophozia ventricosa, L. barbata,* etc. and was fruiting abundantly on Oct. 21, 1945.

The usually easily determined paroecious inflorescence and the abundant fertility, help to distinguish this species. The small size, nearly circular or rounded-ovate leaves (Pl. 8, fig. 3) bearing relatively few purple, stellate gemmae (Pl. 8, fig. 5) at their tips, the thin cell-walls (Pl. 8, fig. 6), and relatively large cells, distinguish it from our other forms. At once separated from *L. bicrenata* our other paroecious species, by the purple, rather scarce gemmae, the crenulate perianth-mouth, and thin-walled cells. Furthermore, *L. excisa* has the stem with a distinct dorsoventral differentiation of the medulla while *L. bicrenata* has the stem only about 8 cells high with no indication of a small-celled ventral band of cells. Both species agree in frequenting similar sites; they are often pioneers on loamy or clayey soils (i.e. substrates poor in organic matter) or on such soils occurring in crevices of cliffs or rocks or on rock-talus; both are able to tolerate rather direct insolation.

Both Müller (1939) and Buch (1941) place this species in the subgenus *Massula.* Such a disposition seems unwarranted to the writer since all other species of *Massula* examined have a uniform medulla of the stem while *L. excisa* has it distinctly dorsoventrally differentiated. Buch (1944) also notes the distinctly dorsoventrally differentiated stem of this species. Müller (1939) placed the species in *Massula* because of a fancied resemblance of the oil-bodies to those of *Massula.* I find they are quite similar to those of *Dilo-*

* See Appendix, p. 703.

phozia and furthermore consider the stem-structure a more fundamental feature.

Subgenus MASSULA K. Müll.[26]

L. (MASSULA) MILDEANA (Gottsche) Schiffn.*

Rare: TOMPKINS CO.: South Hill Marsh, *R. M. & O. M. Schuster;* near Sixmile Creek, *A. L. Andrews;* Ringwood Swamp, *R. M. & O. M. Schuster;* McLean Bogs, on the ground, *A. L. Andrews.*

GENESEE CO.: Along marly ditch, Bergen Swamp, *R. M. & O. M. Schuster?*

This species is confined to wet, swampy or marshy areas; it rarely occurs on well-drained soil or sandy to gravelly ground along ditches as at Bergen Swamp, there associated with such calciphiles as *Preissia quadrata* and *Equisetum varietatum.* At the South Hill locality it occurs under more typical conditions: on moist, sandy-loamy, acid soil at the edges of the marsh with *Scapania irrigua* and *Lophozia (Isopaches) bicrenata.* At the Ringwood locality it occurred on a very rotten log lying in shallow water, with such species as *Lophozia porphyroleuca, Odontoschisma denudatum* and *Cephaloziella elachista.* It does not form a close union with these however, but is closely associated with *Polytrichum* (a moss whose height and usually densely caespitose habit offer it the necessary shade); the correlation between the occurrence of the *Polytrichum* and the *L. mildeana* is striking. Both are normally decided calciphobes, occurring on acid and often sterile soils. The hygrophytic habit and lack of any degree of tolerance for direct sunlight limit the occurrence of the plant; under conditions of direct light as on open ground near the marshes, it may occur densely covering moist loamy soil around the bases of sedges and grasses where it is sufficiently shaded.

The lax leaves with a large-meshed cell net (40-50 μ), the rather transparent appearance, light green color, usually somewhat reddish-tinged in exposed areas, differentiate this species. The occurrence of some leaves at least that are 3-lobed allies it to *L. marchica,* from which it is sometimes difficultly separable; the lack of any purple pigmentation of the stem separates the two; furthermore, *marchica* appears confined to *Sphagnum*-bogs and never develops any pigmentation of the leaves or perianth.

L. (MASSULA) MARCHICA (Nees) Steph.

Rare and local: SENECA CO.: Junius Sphagnum Bogs, 1945, *Schuster.*

Apparently entirely confined to the moors of peat-bogs. It grows here as isolated plants or as an often tangled, thin, loose mat, with both stems

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26 Müller described this subgenus as a segregate from *Dilophozia,* to include the species formerly placed in the latter that had small (2-4 μ) oil-bodies which occurred in large numbers in each cell (mostly 25-50 per cell). There are also other differences that seem to warrant the acceptance of *Massula:* the included species normally have a tendency under xeric conditions, to develop equally thick-walled leaf-cells; the leaf cells are relatively larger; the perichaetial bracts are usually dentate; the stem has a uniform medulla with the ventral cells not even slightly smaller than the dorsal. The latter characteristic is noteworthy in that it indicates the classification of Buch of the Lophozioid complex into two basic groups, depending on medulla structure, *cannot* be accepted without much change.

* See Appendix, p. 703.

and leaves contorted and undulate, crawling over *Sphagnum. Cephaloziella elachista, Calypogeia sphagnicola, Mylia anomala* and *Cladopodiella fluitans* are the usually associated species. At Junius it grows together with the rare *Lycopodium inundatum* and with *Utricularia cornuta,* northern species not reaching much further south. The species is a typical member of the *Mylia* Associule, generally disappearing as trees succeed the *Chameadaphne* Heath.

The very lax, wavy and undulate, mostly 3-lobed, pale-green, semi-translucent leaves (Pl. 9, fig. 1), with cells 40-50 μ, and the always purplish stem (at least beneath), as well as the habit, are more than sufficient to distinguish the species. The very numerous minute (2-4 μ) oil-bodies, appearing like minute glistening, homogeneous spheres, characterize this species (and *mildeana* and *incisa*).

L. (MASSULA) INCISA (Schrad.) Dumort.

Very scarce: TOMPKINS CO.: Enfield Ravine, 1894, *Wiegand;* Coy Glen, *A. L. Andrews;* Ellis Hollow Swamp, *A. L. Andrews.* MADISON CO.: Nelson Bog, *fide A. L. Andrews.* CORTLAND CO.: Beaver Brook, south of East Cortland, *A. L. Andrews.* CHENANGO CO.: Plymouth Bog, near S. Plymouth, *Schuster & Rader.* GENESEE CO.: Bergen Swamp, *R. M. & O. M. Schuster.* ONONDAGA CO.: (Onondaga) Valley (Goodrich 1912, p. 22); Jamesville, with *Calypogeia neesiana meylanii* and *Jamesoniella, Underwood,* 1890; also mixed among Underwood & Cook, Hep. Amer. No. 77, which also contains *Tritomaria exsectiformis* (not *exsecta*), *Blepharostoma* and a little *Harpanthus scutatus.* ONTARIO CO.: Briggs Gully, Richmond, *R. M. Schuster.* CORTLAND CO.: Truxton, with *Tritomaria exsecta,* Wiegand, 1893.

A typical member of the mesophytic xylicolous associule of the Transition and Canadian Zones, associated with *Lophozia porphyroleuca* (as at Bergen Swamp), *Harpanthus scutatus, Riccardia latifrons, Cephalozia connivens, Odontoschisma denudatum,* etc. At higher altitudes and latitudes, the species also grows on peaty soil among mosses.

The thick, succulent stems, crispate, sharply lobed leaves, often on the upper leaves with spinous, scattered teeth as well as the opaque, bluish-green color (due to the very densely chlorophyllose cells) and small size, differentiate this species. It does not look very much like a *Lophozia.* Perhaps a comparison with *Scapania apiculata* would bring a more accurate picture to mind. (Pl. 8, figs. 11-13).

Subgenus ISOPACHES Buch

L. (ISOPACHES) BICRENATUS (Schmid.)

Locally common: TOMPKINS CO.: Coy Glen, *R. M. & O. M. Schuster;* southwest corner of Cayuga Lake, *Nanz;* Sixmile Creek Ravine, *R. M. & O. M. Schuster;* Buttermilk Glen, *R. M. & O. M. Schuster;* Old Buttermilk Glen, *R. M. & O. M. Schuster;* Taughannock Gorge, *R. M. Schuster;* Enfield Glen, *R. M. & O. M. Schuster;* Lick Brook, *R. M. & O. M. Schuster;* Fall Creek Ravine, *R. M. Schuster;* McKinney's Twin Glen, *R. M. & O. M. Schuster;* Esty Glen, *R. M. & O. M. Schuster,* South Hill, *R. M. Schuster.* SENECA CO.: Sandy sterile soil around Junius bogs, *R. M. Schuster.* ONTARIO CO.: Briggs Gully, *R. M. Schuster.* CATTARAUGUS CO.: Nichol's Run, *Limestone;* Bonaventure (Boehner 1943, p. 13); Mt. Moriah, with perianths, *Boehner,* det. by Schuster.

Typically occurring on leached, sterile soils at the ravine crests where it is subject to long periods of drought during the summer months; occurring there usually on exposed loamy soils. Commonly, almost invariably in fact, are associated *Cephaloziella rubella* (*myriantha*) and very frequently, in slightly

moister situations, *Lophocolea minor*. *L. (Barbilophozia) barbata* at its only locality where I know it to be abundant, grows with the *Isopaches* as well as the other two species. On the more flat, sandy Ontarian plain, it occurs directly on the sterile, acid soils, associated with the *Cephaloziella*. On South Hill marshes it occurs on moist, exposed soil and with *Plectocolea crenulata*. At Lick Brook it occurs in the crevices of exposed cliffs together with *Tritomaria exsectiformis* and the *Cephaloziella* as well as with *Lophozia ventricosa*.

The more xeric habitats preferred by *L. bicrenatus* often separate it from our other *Lophozia* with a paroecious inflorescence — *L. excisa*; the latter furthermore, has purplish gemmae while the present species has them reddish or brownish-yellow. The thick cell-walls, in exposed situations so thick that the cell-lumen appears guttulate (Pl. 8, fig. 14), also separates the species. Usually sterile shoots can be found with numerous gemmae; such shoots usually have the lower leaves irregularly dentate and often somewhat lobed, due to gemmae formation.

The species is nearly constantly fertile, perianths being produced in abundance. These are distinctly ciliate-dentate at the mouth (unlike those of *excisa*) and formed of guttulate, very thick-walled cells. When doubtful sterile material is at hand both of these orbicular-leaved species are hard to separate. The almost circular leaf-shape (with a shallow, lunate or obtuse sinus) is common to both species but does not occur in our other species of *Lophozia*. Stem cross-sections easily differentiate *bicrenata*: they are merely 8 cells high (or thereabouts) and the medulla consists of uniform cells. Much of the material found has perianths and capsules: the latter have incomplete or semiannular thickenings of both the inner and outer cell-layers (all our other *Lophozia* species have complete annular thickenings of the inner cell-layer while the outermost layer only has nodular thickenings). *L. bicrenata* also has the capsule-wall bistratose while our other species of Lophozia (s. str.) have the wall 3-5 cell-layers thick. These differences in the capsule-wall are perhaps sufficient to warrant retaining *L. bicrenata* in a separate subgenus.

II. TRITOMARIA Schiffn.

The present genus is accepted with some misgivings. The dorsiventrally differentiated medulla indicates it is to be derived from the subgenus *Dilophozia*. The similarity between such species as *Lophozia longidens* and *Tritomaria scitula* is such as to make one doubt the wisdom of attempting a generic separation. The subgenus *Lophozia* often produces occasional subequally trilobed leaves that scarcely allow any differentiation from those of *Tritomaria*. The leaf-insertion in lax-leaved forms of *T. scitula* as well as in *T. quinquedentata* is distinctly succubous: at most the dorsal fourth of the insertion being transverse; in our two species it is transverse, however. Furthermore, such species as *T. scitula* often produce occasional 2-lobed leaves, similar entirely to those of *Lophozia*. Where one is to draw a sharp differentiation here seems difficult to appreciate; therefore the writer feels that *Tritomaria* should perhaps be considered nothing more than a subgenus of *Lophozia*.

As is indicated in the key to subgenera of the complex, I do not recognize *Saccobasis* as generically distinct from *Tritomaria*. It represents merely the end-product of a developmental line leading from the subgenus *Lophozia* to *Tritomaria* (subg. *Eutritomaria*) to *Saccobasis*.

T. (EUTRITOMARIA) EXSECTA (Schmid.) Schiffn.

Rare locally. TOMPKINS CO.: Enfield Glen, *R. M. & O. M. Schuster*. CORTLAND CO.: Robbins Glen, Truxton, *Wiegand*. ONONDAGA CO.: Jamesville (Underwood and Cook, Hep. Amer. No. 72, 1890). (At least the specimen of Underwood & Cook's Hep. Amer. No. 77 in the University of Minnesota herbarium is *T. exsectiformis;* since the two species often occur intermingled, some of the material of this number may have been true *exsecta*). CATTARAUGUS CO.: One mile north of Rock City, *Schuster & Rader;* Martiny Rocks, West Branch of Four Mile Road, Allegany (Boehner 1943, p. 13).

This species occurs locally on semi-exposed to shaded, moderately moist to intermittently dry cliffs and ledges, usually as a chasmophyte or on thin soil over bare rock. Here it is usually associated with *L. bicrenata, L. ventricosa, Cephaloziella rubella, hampeana* and *Scapania nemorosa,* occasionally with *Jamesoniella.* On the quartz-conglomerate of Rock City, it occurred in addition, with such locally "calcifugous" species as *A. michauxii* and *A. minuta,* under which its ecology is discussed. Also frequently occurring on decaying wood with *Jamesoniella, Harpanthus* and other xylicolous species. This species is more common in the Canadian Zone and locally rarely occurs in any quantity. With only a minute tolerance for lime; its local rarity is perhaps due largely to this fact.

The transversely inserted leaves with two lobes or teeth at the leaf apex (Pl. 9, fig. 4) and usually a third tooth on the antical margin (i.e., unequally 3-lobed) as well as the red or reddish-brown gemmae masses at the apices of the plant, separate this and the following species from all other local Hepaticae. The smooth, ovoid (rather than angulate), relatively small gemmae (Pl. 9, fig. 5) and the much smaller size of the cells, distinguishes this species from the next.

T. (EUTRITOMARIA) EXSECTIFORMIS (Breidl.) Schiffn.*

Rare. CATTARAUGUS CO.: about one mile north of Olean Rock City, October, 1945, *R. M. & O. M. Schuster, W. Rader;* Martiny Rocks, West Branch of the Four Mile Road, Allegany (Boehner 1943, p. 13). ONTARIO CO.: Briggs Gully, Richmond, *R. M. Schuster.* ONONDAGA CO.: Jamesville, June 1890 (*L. M. Underwood*). TOMPKINS CO.: Rice Brook, *R. M. & O. M. Schuster.* CHENANGO CO.: abundant on decaying, peaty logs at sphagnous edge of Plymouth Pond, with *Scapania paludicola, Jamesoniella, Lophozia porphyroleuca,* etc., *Schuster & Winne.*

This species as regards the known distribution, appears to be more northern than *T. exsecta.* It occurs under similar conditions but perhaps more rarely on decaying wood, often on vertical rocks associated with *T. exsecta* (as at Rock City) and such northern species as *Bazzania denudata, A. minuta, A. michauxii* and *L. ventricosa.* Almost invariably associated with *Scapania nemorosa.* Evidently far more frequent in our area than *T. exsecta* and when found often in moderate quantities and occasionally in pure

* See Appendix, p. 703.

patches. With little or no tolerance for lime; its local rarity is perhaps largely a result of this fact. Apparently a little more of a xerophyte than *exsecta* and able to tolerate considerable amounts of direct sunlight.

Superficially indistinguishable from *T. exsecta*. Under the microscope the cells are seen to be half again as long as in *exsecta* (22-36 μ or more long in the leaf-middle) with the trigones often bulging; the gemmae are also much larger than in *exsecta* and are angular, not ovoid (Pl. 9, fig. 7).

Since this species was not distinguished before 1893 (and even later in North America), the earlier reports of *exsecta* should be reexamined since they certainly in part belong there. As is stated under *exsecta*, the Underwood & Cook issue of *exsecta* belongs here at least in part. I have also not had recent opportunity to check Wiegand's report of *exsecta* from Cortland County, which may well belong with *exsectiformis*. I have had opportunity to study some of Boehner's material from Martiny Rock, which grew associated with *Jamesoniella, Plagiochila* and *L. gracilis*.

III. ANASTROPHYLLUM (Spr.) St.

Müller (1947a) states that he believes *Crossocalyx* could have been well left within *Sphenolobus*. I would go even further and not give *Sphenolobus* generic recognition, but consider it as a mere subgenus of *Anastrophyllum* (the older name, generically). Essentially *Anastrophyllum* and *Sphenolobus* differ only in that the former has the dorsal lobe distinctly decurrent,[27] while the latter has it quite transverse in insertion. This does not seem enough to the writer to make recognition of a genus feasible. I therefore would include three subgenera within *Anastrophyllum*: *Crossocalyx, Sphenolobus* and *Euanastrophyllum*. The separation between these is given in the key to the Lophozioid complex.

Subgenus CROSSOCALYX Meylan

A. (Crossocalyx) hellerianus (Nees) comb. n.

Very rare locally. TOMPKINS CO.: Coy Glen, *A. L. Andrews;* Lick Brook, on bark of *Tsuga*, 5-8 feet above ground, *Schuster & W. Scudder*. ONTARIO CO.: Briggs Gully, *Schuster*. CAYUGA CO.: Paines Creek, *Schuster & Andrews*.

A species occurring only as a rarity south of the Canadian Zone; appearing even more rare because its minute size and general occurrence as small, isolated patches or plants, results in its being generally overlooked. Locally it is limited to the ravines where the temperature approaches more nearly "Canadian Zone" conditions and appears to be the chief factor that enables it to survive here. Typically a member of the *Nowellia-Jamesoniella* Associule of moist, decaying logs together with *L. porphyroleuca, L. incisa, Scapania apiculata* and *glaucocephala, Jamesoniella autumnalis* and *Harpanthus*

27 This is definitely the case in spite of the fact that our local species is separated by Frye and Clark (1945, p. 393) as having the "leaves not decurrent." Furthermore, *Sph. saxicolus* also has the dorsal lobe more or less decurrent (especially on lax-leaved shoots), thus bridging the gap between *Sphenolobus* and *Anastrophyllum* (as delimited by Buch 1933). Perhaps the most fundamental gap lies between *Sph. saxicolus* and *A. michauxii* (with 3-5-stratose capsule-wall) and *Sph. minutus* and *C. hellerianus* (both with 2-stratose capsule-wall).

scutatus; occurring very frequently with the latter species. In the various texts and reference works this species is generally listed as occurring only on rotten logs; that is, decorticated, fallen logs in process of decay. This is not strictly true since I have found it five to eight feet above the ground, occurring in crevices of the bark of hemlock *(Tsuga canadensis)* in a dense, shaded, ravine bottom as a leptodermous modification, with cells 10-12 x 12-16 μ. Such leptodermous modifications are scarcely typical since they produce relatively few of the erect, reduced-leaved, slender gemmiparous shoots so characteristic of the species. The characteristic gemmae are here produced in abundance at the tips of simple ascending shoots bearing normal, nearly full-sized leaves.

The minute, vineous-red, mostly quadrate gemmae, 10-11 μ in size (Pl. 7, fig. 6), occurring in masses on erect, more or less attenuate shoots bearing erect, appressed, minute leaves (Pl. 7, fig. 4) together with the small size of the plant and the subtransversely inserted leaves easily characterize this species. The minute size is alone sufficient to separate the species from all other local lophozioid species; the plants often not exceeding 3-5 mm in length.

Subgenus SPHENOLOBUS Lindb.

A. (Sphenolobus) minutus (Crantz) comb. n.

Very rare. TOMPKINS CO.: Coy Glen, *Jackson*, 1903. CATTARAUGUS CO.: north of Rock City, Oct. 1945, *R. M. Schuster & W. Rader;* Olean Rock City and Martiny Rocks, West Branch of the Four Mile Road, Allegany (Boehner 1943, p. 13).

A typically Canadian-Hudsonian species, locally a relic of the glacial period. Occurring without much doubt into western Pennsylvania since it occurs within 2-3 miles of that state at Rock City but unreported for that state by either Porter or Lanfear.

At Coy Glen, the species was collected on a rotting log; I have been unable to rediscover the species here. The Cattaraugus County record is of material occurring on the vertical faces of moist-to-wet quartz-conglomerate ledges together with such Canadian-Hudsonian species as *Anastrophyllum michauxii, L. (Orthocaulis) gracilis* and *Bazzania denudata.*

The rarity of the species in our area is essentially due to the absence of any considerable amounts of siliceous rocks in our area as well as to the absence of elevations higher than 2500 feet, below which *L. minutus* occurs only exceptionally in areas approaching the Transition Zone. The Coy Glen record is therefore of much interest since it is at an elevation of 450-800 feet.

The species is a member of the *Nowellia-Jamesoniella* Associule of rotting logs, associated with such forms as *Nowellia, Lophozia porphyroleuca, Cephalozia* spp., *Blepharostoma* and *Odontoschisma denudatum,* as well as of the meso-xerophytic saxicolous associule of mostly non-calcareous rocks, there associated with such species as *Diplophyllum apiculatum, Lepidozia reptans, Blepharostoma, Anastrophyllum michauxii, Scapania nemorosa, Bazzania denudata, Tritomaria exsecta* and *exsectiformis, Jamesoniella autumnalis,* etc.

The slender, filiform appearance with the complicate-concave leaves regularly, pectinately inserted on each side of the stem (Pl. 9, fig. 8) in an almost horizontal plane, as well as the smaller size (compared with *A. michauxii*),

easily differentiate this species. In our area where both *minuta* and *michauxii* occur near their southern limits (biogeographically), the two frequently approach each other in size and distinction occasionally may be difficult for the beginner. *A. minuta* can be told at once however, by the fact that gemmae occur at the apices of more or less reduced, somewhat deformed, erect or erect-appressed leaves, occurring at the upper parts of gradually slender, filiform shoots which when developed well, appear rather similar to those of *A. helleriana*. When *michauxii* bears gemmae, these are at the apices of normal, spreading, unreduced leaves; the gemmae are also darker, more purplish, contrasted to the bright red, occasionally almost scarlet gemmae of *minutus*. The less evenly thickened walls of the leaf-cells also at once separate *michauxii* (Pl. 7, figs. 12, 13) from the present species (Pl. 9, fig. 10).

Subgenus **Euanastrophyllum** subg. n.

A. (EUANASTROPHYLLUM) MICHAUXII (Web.) Buch

Very rare. CATTARAGUS CO.: one mile north of Rock City, 1945, *Schuster & Rader;* Martiny Rocks, with *A. minutus* and *L. gracilis, Boehner,* det. by *Schuster.* ONONDAGA CO.: Peppermill Gorge (Goodrich 1912, p. 22).

Also very northern in distribution, occurring only exceptionally into the Transition Zone; a montane and submontane species. Its apparent inability to tolerate lime as well as its inability to survive below 1800-2000 feet as one approaches the Transition Zone, appear to indicate that the Onondaga County record may be incorrect.

At Rock City occurring at 2400 feet on moist-to-wet quartz-conglomerate ledges, intimately associated with *A. minutus, Scapania nemorosa, Bazzania denudata,* and *T. exsecta* and *exsectiformis.* Almost certainly occurring in western Pennsylvania though unreported from there. A typical Canadian-Hudsonian species, occurring largely on decaying logs, usually in an advanced state of decay; more rarely, on humus and on thin soil on cliffs and ledges.

The rather large size, bilobed leaves mostly widest near base (Pl. 7, fig. 14) and the strongly succubous insertion of the lower half of the leaf, contrasted with the transverse and decurrent insertion of the dorsal half, will identify this species. The large, usually bulging, yellowish trigones of the leaves are characteristic (Pl. 7, figs. 12, 13) and separate it at once from most of our other bilobed-leaved Lophoziae.

Not reported for Cattaraugus County by Boehner (1943).

IV. GYMNOCOLEA Dumort.

G. INFLATA (Huds.) Dumort.

Very rare locally. TOMPKINS CO.: Cayuga Heights, Crest of Fall Creek Ravine, 1943, *Schuster;* "Ithaca" (*Holzinger,* 1901), reported by Frye and Clark 1945, p. 369; Taughannock Gorge, *Andrews, Schuster.**

A species much more typical of the Canadian-Hudsonian flora, extending well into the Arctic-alpine Zone. Locally it is found on the acid, sterile crests

* See Appendix, p. 703.

of the ravines (Fall Creek), a member of the *Chestnut-Oak-Vaccinium* Associes or on non-calcareous disintegrating shale ledges and talus (Taughannock). Apparently able to tolerate small quantities of lime since the calciphilous *Lophozia badensis* occurs with it at Taughannock. *Scapania mucronata, S. nemorosa, Cephalozia bicuspidata, Cephaloziella byssacea* and var. *scabra,* are found associated with it. Of these, *Scapania nemorosa* and *C. bicuspidata* are almost constantly found with it in the New England States. Hygrophytic or meso-hygrophytic with a considerable tolerance for direct sunlight.

The rounded lobes of the subcircular bilobed leaves (Pl. 9, figs. 11, 13-14), the dark to purplish-green or blackish color and the presence of lateral branching separates this species from all other local forms. *Cladopodiella* is very similar in facies but occurs only in bogs and has ventral branches. The caducous inflated, sterile perianths of *Gymnocolea* (Pl. 9, fig. 14), present almost invariably, are a unique feature that easily separate it from all other species.

V. JAMESONIELLA (Spruce) Steph.

J. AUTUMNALIS (D. C.) Steph.

Rather common, widely distributed. TOMPKINS CO.: Sixmile Creek; McLean Bogs; three miles south of Dryden; Woodwardia Bog; Freeville Fir Tree Swamp; Malloryville Bog; Ringwood; Enfield Glen; Coy Glen; South Hill Marsh; Cascadilla Glen; Fall Creek Ravine; Pony Hollow, Newfield; Michigan Hollow Swamp; Headwaters Swamp; near source of Sixmile Creek. CHEMUNG CO.: Bog 1 mile from southwest corner of state; Van Etten. CATTARAUGUS CO.: north of Rock City, Oct. 21, 1945, in abundant fruit; Martiny Rocks, Allegany; Waterman Swamp, Napoli, etc. CAYUGA CO.: Paines Creek near Aurora. GENESEE CO.: Bergen Swamp. ONONDAGA CO.: Salt Marsh (Goodrich 1912, p. 22, as *Jungermannia schraderi*); Syracuse (Underwood & Cook, Hep. Amer., No. 18, as *J. schraderi*); Jamesville. ALLEGANY CO.: near Alma. MADISON CO.: Chittenango Falls. CORTLAND CO.: Kenney Creek Gulf, Truxton; east of Solon. TIOGA CO.: southern part of Headwaters Swamp. CHENANGO CO.: Plymouth Reservoir and Bog, near S. Plymouth.

A type member of the *Nowellia-Jamesoniella* Associule of moist, somewhat-to-strongly exposed decaying logs, associated with *O. denudatum, Lophozia porphyroleuca, Nowellia, Harpanthus scutatus, Riccardia latifrons,* and occasionally *T. exsectiformis, A. helleriana,* and *T. exsecta.* Widespread also on sterile, acid, exposed soils as on the crests and sunny slopes of ravines, on thin soil over ledges and cliffs and around the bases of trees; rarely invading the butts of trees above the roots. In our area occurring only rarely on rocks (Sixmile Creek and Briggs Gully), largely because of the decided preference the species has for siliceous rocks. However, on the quartz-conglomerate, moist, ledges of Rock City it is an abundant species, forming extensive, luxurious mats, much as in most siliceous regions; here it occurs with *Bazzania denudata, Lophozia gracilis, T. exsecta, T. exsectiformis, A. minuta* and *A. michauxii,* entering into the characteristic *Scapania-Lophozia* Associule of siliceous, moist ledges, accompanied by the characteristic accessory species *Lepidozia reptans, Blepharostoma* and *Bazzania denudata.*

When sterile, easily confused with other entire-leaved species by the be-

ginner. The frequent occurrence of a few retuse or emarginate leaves (Pl. 10, fig. 1, r), the rounded-rectangular shape of the leaves and the absence of bulging trigones will separate the species. *Jungermannia lanceolata* is similar in size and rather similar in facies; the larger trigones, elongate, never retuse leaves and the absence of reddish pigmentation, separate the latter species. The absence of erect, gemmiparous shoots and the smaller, never bulging trigones, separate the species from *Odontoschisma*. When fertile, the ciliate perianth-mouth and presence of cilia at the bases of the bracts (Pl. 10, figs. 2-4), will at once separate *Jamesoniella*. The plants are dioecious and usually only plants of one sex occur in a patch. The male plants which have compact, obvious androecia (distinctly narrower than the sterile portions of the shoots) which are usually reddish pigmented even in shade forms, are very characteristic. Unlike our other genera of the family Jungermanniaceae with entire leaves (i.e., *Jungermannia, Plectocolea*), *Jamesoniella* bears small underleaves; these can usually be demonstrated only by study of the postical stem surface with the monocular microscope.

VI. JUNGERMANNIA (Ruppius) L.

KEY TO SPECIES

1. Large species, 2-3 cm long; leaves elongate, rectangular-rounded to ovate (Pl. 11, fig. 9), with usually bulging trigones (Pl. 11, fig. 8); perianth cylindrical, terete, smooth, suddenly cntracted to a short-rostrate mouth set in a depression of the truncate apex; oil-bodies 4-19 per cell; paroecious (Pl. 11, fig. 9) ..... *J. lanceolata*

1. Smaller species, rarely to 1.5 cm long; leaves round or ovate to oblong, without or with minute trigones; perianth not smooth, not cylindrical, more or less plicate near apex, not depressed at mouth 2

2. Leaves round, not longer than wide; trigones entirely absent, the pellucid cells 35-40 x 40-50 μ in leaf-middle, very thin-walled; gemmae often present in internal, large, brownish-green masses at the globular apices of shoots; perianth rostellate at mouth; light green plants; dioecious; oil-body to 8-10 x 20 μ, one per cell ..... *J. caespiticia*

2. Leaves longer than wide, ovate or oblong to cordate, none ever retuse at apex; minute trigones often present, the cells mostly less than 40 μ long in leaf-middle; gemmae absent; oil-bodies several per cell; perianth not rostellate; dark green or deep olive green plants 3

3. Dioecious; cells 20-40 μ in leaf-middle; leaves ovate to oblong, not cordate basally; perianth clavate ..... *J. tristis*

3. Paroecious; cells 16-30 μ in leaf-middle; perianth fusiform or leaves cordate 4

4. Leaves of fertile shoots not cordate at base, narrower; cells mostly 23-30 μ in leaf-middle; perianth fusiform, very gradually narrowed to mouth ..... *J. pumilla*

4. Leaves of fertile shoots and of well-developed sterile shoots broadly cordate at base; cells of leaf-middle mostly 16-21 μ; perianth suddenly contracted to apex, more cylindrical-clavate ..... (*J. schiffneri*)

J. LANCEOLATA L.

Rather scarce locally. TOMPKINS CO.: Coy Glen, 1908, *Andrews*, 1946, *Schuster;* Sixmile Creek Ravine, 1942, *Schuster;* Enfield Glen, 1945, *Schuster;* ravine in South Danby, 1945, *Andrews & Clausen.* ONONDAGA CO.: White Lake, Dewitt, on rotten log, 1916, *Wiegand;* Dewitt (Goodrich 1912, p. 23); Kirkville (Underwood & Cook, Hep. Amer. No. 114, as *Liochlaena lanceolata*). MONROE CO.: Irondequoit Bay near Roches-

ter, 1945, *R. M. & O. M. Schuster*. ONTARIO CO.: Briggs Gully, Richmond, 1945, *Schuster*. CHENANGO CO.: rotting log with *Riccardia palmata*, Plymouth Bog, *Schuster*. CHEMUNG CO.: Van Etten (Hep. of the Upper Susquehanna No. 4, *Barbour*).

This species occurs not too rarely on shaded slopes in the ravines, on shady, sandy, moist soil or on humus or decaying logs; occasionally it occurs on humus over thin soil, over shale or sandstone, if the underlying rocks are not calcareous. Apparently with a rather low tolerance for lime. Commonly associated species are *Blepharostoma trichophyllum, Plagiochila asplenioides, Cephalozia media;* occasionally associated are *Lepidozia reptans, Jamesoniella autumnalis* and *Calypogeia trichomanis*. Fruiting abundantly and with ripe capsules on the following dates locally: April 22, April 29, May 14; Ammons (1940) gives May-October (evidently in error) while Macvicar (1926) states March-April.

When sterile, very similar in appearance to *Jamesoniella*; the often retuse leaves of the latter and the smaller cells (25-35 μ, rather than 35-42 μ) with smaller, never bulging trigones, separate the latter. From poorly developed forms of *Plagiochila* the present species may be separated by the non-decurrent antical leaf-margins and the lack of any tendency for the leaves to be reflexed along their antical margins. When fertile, the paroecious inflorescence and the peculiar perianths are characteristic (Pl. 11, figs. 8, 9).

J. CAESPITICIA Lindenb.

Exceedingly rare. ONTARIO CO.: Briggs Gully, Richmond Township, near the lower end of Honeoye Lake, October 1945, *Schuster*.

One of the rarest of North American Hepaticae, reported only twice before (Illinois and Cape Nome, Alaska) outside of Europe; apparently everywhere among the rarities of the hepatic flora. The station above occurred on thin, rather clayey, wet soil over disintegrating shale, on the north-facing side of a ravine. Immediately associated species were *Cephalozia lammersiana, Scapania nemorosa, Diplophyllum apiculatum* and *Calypogeia trichomanis*. Occurring in some quantity, partly on clayey soil, other, small patches, or isolated groups of individual plants, directly in crevices of the shale-fragments. Immature perianths, showing the crenulate mouth as well as the characteristic brownish-green globular gemmae-masses of the apices of the shoots were present. There is no doubt but that this species is at hand since the large size of the leaf-cells (35-50 μ), leaf-shape, absence of trigones, shape of the immature perianths and in particular, the peculiar gemmae-masses, all indicate the present species. Müller (Rabenhorsts Krypt. Fl., 6(1): 544, 1909) considers the species to be a xerophyte and mesophyte; the local occurrence is under decidedly more meso-hygrophytic conditions. Occurring under non-calcareous conditions.

Differs from all other entire-leaved Hepaticae in the presence of large, globose heads at the stem-apices, closely surrounded by a pair of leaves, within which gemmae arise endogenously. The gemmae in the present collection were about 10-12 x 12-15 μ, roundish-quadrate, one-celled, thin-walled and rather hyaline. Otherwise closely similar in appearance to *P. crenulata*, except that it lacks the border of large cells of the leaves and lacks the thick cell-walls of that species. The yellow-green color, circular leaves, rather small

size, long, hyaline, colorless rhizoids, all suggest a form of *P. crenulata* lacking the bordered leaves. The extremely large oil-bodies occurring one per cell are very characteristic.*

J. PUMILLA Wither.

Very rare locally. ONONDAGA CO.: Peppermill Gorge (Goodrich 1912, p. 22). CATTARAUGUS CO.: on rocks at Pumpkin Hollow, Five Mile Road.

The local rarity of this widespread species may be directly influenced by its "calciphobous" nature. The species is meso-hygrophytic and usually occurs on moist or wet rocks.

The dark green color (occasionally rather olive green) and the ovate or broadly elliptical leaves, not cordate at base, with the cells not over 30 μ in the leaf-middle, distinguish this species. Confusion is likely only with *J. tristis* which has similar leaves, but a strongly clavate or obpyriform perianth (not spindle-shaped) and somewhat larger cells and is dioecious.

The record of the species from Onondaga County needs confirmation since the inclusion of so many erroneous reports in the Goodrich catalog makes it hazardous to accept any records therein on faith.

J. TRISTIS Nees

Very rare. CATTARAUGUS CO.: on stones near a creek at Martiny Rocks, West Branch of Four Mile Road, Allegany (Boehner 1943, p. 13); not seen by writer.

The only other record of this species from the eastern states is that for North Carolina (Frye & Clark, 1937-1947, p. 293). This species apparently has some toleration for lime and in some regions appears to be a pronounced calciphile.

The ovate to oblong leaves, dark green color and the rather large cells (about 20 x 40 μ), characterize this species; it differs from our other members of this section of the genus in the dioecious inflorescence and strongly clavate perianth.

(J. SCHIFFNERI Loitlesb.

Occurring to our south in Western Pennsylvania; perhaps to be expected in our area.

Similar in color and appearance to *J. pumila* but with well-developed leaves cordate, broader than in that species, and with the cells distinctly smaller; the perianth is not at all fusiform.)

VII. PLECTOCOLEA Mitt.

KEY TO SPECIES

1. Leaves with a distinct border of large, swollen cells two to three times as large as those immediately interior to them (Pl. 10, figs. 7-8); rhizoids pale; leaves not undulate; perianth deeply 4-5-folded, beaked ..... *P. crenulata*

1. Leaves lacking any border of larger cells, the marginal cells equal to the interior in size; rhizoids reddish; upper leaves undulate; perianth weakly plicate apically ..... *P. hyalina*

P. HYALINA (Lyell.) Mitt.

Very rare. CATTARAUGUS CO.: on rocks near a creek, Pumpkin Hollow, Five Mile Road, Allegany (Boehner 1943, p. 13); not seen by writer.

* See Appendix, p. 703.

This species apparently is absent from our region except in the area of the Appalachian plateau, although it can tolerate distinctly calcareous conditions. Like the section Luridae of *Jungermannia*, the present species occurs on moist or wet rocks, often subject to inundation; less frequently it occurs on wet soil at the edges of streams and brooks.

This species is likely to be confused with species of *Jungermannia* or with *Jamesoniella*. The reddish rhizoids at once differentiate it from both of these genera, among our Hepaticae only *Fossombronia* possesses similarly colored rhizoids. The perianth which is fused at its base with the bracts and is hidden largely between them, is also characteristic.

P. CRENULATA (Sm.) Evans*

Frequent locally. CATTARAUGUS CO.: St. Bonaventure; South Branch of Cattaraugus Creek, Gowanda; Waterman Swamp, Napoli; Nichol's Run; Limestone (Boehner 1943, p. 13). TOMPKINS CO.: South Hill, *R. M. & O. M. Schuster;* Sixmile Creek, with mature capsules, March 29, 1946, *Schuster;* Varna, *Schuster;* Beebe Lake in Ithaca, *R. M. & O. M. Schuster;* Enfield Glen, *R. M. & O. M. Schuster;* two miles south of Dryden, *R. M. & O. M. Schuster.* ONONDAGA CO.: Onondaga Hill (Goodrich 1912, p. 23).

Probably widely distributed on loamy, moist banks throughout our region, though further records are lacking. With a rather wide tolerance for lime and often occurring in areas also inhabited by *Lophocolea minor* but apparently most common on sandy-loamy, leached, exposed, sterile soils especially of periodically denuded banks. Here it is associated most often with such species as *Fossombronia wondraczekii, Lophozia bicrenata,* and *Cephaloziella rubella.* On distinctly acid, denuded banks and soil (as on South Hill) it grows with a pachydermous modification of *Scapania irrigua* as well as with the above species and *Lophozia mildeana.* On more decidedly moist banks it is frequently found with members of the *Anthoceros-Blasia* Associule, most often with *Anthoceros laevis* and *crispulus, Blasia* and *Pellia epiphylla.* It is one of the first species to colonize denuded, moderately moist to rather dry, sandy-loamy banks. Its moisture and light preferences are both lower than those of the *Anthoceros-Blasia* Associule and hence it occurs with them usually as an accessory species; its requirements however, are very similar to those of *Fossombronia* and it therefore often forms a distinct *Plectocolea-Fossombronia* Associule of moderately shaded, only moderately moist sandy-loamy soil, either on banks, in the middle of wagon-roads, or at the edges of paths.

P. crenulata can be separated at once from all our other species by the presence of the distinct border of large, swollen cells at the margin of the leaves (Pl. 10, fig. 8) which are characteristically round, entire, hyaline (often reddish-tinged, especially on exposed ground) and usually little chlorophyllose. The perianth (Pl. 10, fig. 7) is characteristic.

VIII. MYLIA S. F. Gray, emend. Carr.

M. ANOMALA (Hook.) Gray

Locally frequent but generally rare. TOMPKINS CO.: McLean Bogs, *Andrews, Schuster & Rader;* Malloryville Bog, *Schuster.* CATTARAUGUS CO.: Swamp near Crystal Lake,

* See Appendix, p. 703, for *P. crenuliformis.*

Boehner, det. Schuster. GENESEE CO.: Bergen Swamp, *E. J. Hill, Schuster*. SENECA CO.: Junius Peat Bogs, *R. M. & Erwin Schuster*. ONONDAGA CO.: Jamesville Road (Goodrich 1912, p. 23, as *M. taylori*—evidently in error for the present species). CHENANGO CO.: Plymouth Bog and Reservoir, near S. Plymouth, *Schuster & Winne*.

This species is locally confined entirely to the open parts of *Sphagnum* bogs. It occurs here as the type member of the *Mylia* Associule, associated with such species as *Cladopodiella fluitans, Cephaloziella elachista, Lophozia marchica, Calypogeia sphagnicola, Cephalozia connivens*, etc. It is one of the first species to colonize and invade to open parts of bogs, subsequent to the colonization by *Sphagnum*. *Cephalozia connivens* and *pleniceps* generally invade much later and are limited more to the outer edges where the ericaceous plants have become rather dense and where the arborescent vascular plants are beginning to take a foothold; they are generally accompanied during the latter stages by *Pallavicinia lyellii* which usually does not invade bogs until arborescent plants provide rather dense shade. *Cephaloziella elachista* is perhaps the most adaptable of the *Mylia* Associule; it is among the first forms to invade, and persists long after both *Mylia* and *Cladopodiella* have been succeeded by a more humicolous flora, and even after the *Sphagnum* itself has died away.

M. anomala can be told from our other species by the restricted occurrence and especially by the fact that the upper parts of gemmiparous shoots bear lanceolate-acuminate to ovate-acuminate leaves, strongly contrasted to the more circular lower leaves (Pl. 11, fig. 1). These gemmiparous leaves furthermore are unique in possessing a group of apical cells (50-60 μ long or more) that are far larger than the already large-sized normal leaf-cells (Pl. 11, figs. 3-4). *Odontoschisma sphagni* which is to be looked for in our area, is rather similar but lacks both the narrow apical leaves and the gemmae; it furthermore has flagellae, absent in *Mylia*.

Family MARSUPELLACEAE

I. MARSUPELLA Dumort.

M. EMARGINATA (Ehrh.) Dumort.

Very rare, doubtfully present in our flora. ONONDAGA CO.: Howlett Gorge (Goodrich 1912, p. 23).

It is very doubtful whether the above record should be accepted; the abundant presence of errors in the Goodrich list, the doubtful presence of *Marsupella* anywhere at low elevations in the Transition Zone, and its largely calciphobous nature all indicate that the present record is very much open to doubt. The species should occur at high elevations in Cattaraugus and Allegany counties but is probably absent from the rest of our area unless the Goodrich record can be substantiated.

A somewhat "calciphobous" species, limited in occurrence to moist cliffs and ledges, subject to innundation, to the edges of waterfalls, and to boulders in streams, chiefly in siliceous regions.

The large size, its hygrophytic nature, the wide, transversely inserted, shortly bilobed leaves (Pl. 11, fig. 7), and the strongly reduced, hidden perianth easily separate this species from all others in our flora. The leaves

are very regularly pectinately inserted, much as in *Sphenolobus*, but they are not canaliculate or concave-complicate (Pl. 11, fig. 5, 6).

Family HARPANTHACEAE

I. LOPHOCOLEA Dumort.

KEY TO SPECIES

1. Upper leaves of most mature shoots retuse to merely emarginate, the lobes rounded, the lower leaves with acute lobes (Pl. 10, fig. 11); gemmae absent; paroecious, usually fertile ..... *L. heterophylla*

1. All the leaves sharply bilobed, the lobes all acute (unless erose through gemmae formation); not paroecious, rarely fertile 2

2. Gemmae always present, giving the plant a dusty, yellow-green appearance; leaves not narrowed towards apex; small, less than 1.5 mm wide (Pl. 10, fig. 9) ..... *L. minor*

2. Leaves never with gemmae at their apices, distinctly narrowed toward the apex (Pl. 10, fig. 10); large 2-3 mm wide ..... *L. bidentata*

L. HETEROPHYLLA (Schrad.) Dumort.

Abundant, ubiquitous. TOMPKINS, CATTARAUGUS, STEUBEN, ONONDAGA, MADISON, MONROE, GENESEE, TIOGA, YATES, CORTLAND, SCHUYLER, ERIE, CHENANGO, CHEMUNG, ALLEGANY, ONTARIO and OTSEGO COUNTIES. ONONDAGA CO.: Jamesville (Underwood & Cook, Hep. Amer. No. 35).

So widespread that any listing of exact localities is superfluous; undoubtedly our most common foliose species, able to tolerate great variations of environmental conditions from very acid to distinctly calcareous, from very shaded to quite exposed, from almost hygrophytic to distinctly xerophytic. Its wide tolerance, indeed, its aggressive nature under many conditions and its ability to at least survive under a multitude of other conditions, combine to make this our most widespread form among the Jungermanniales. Able to invade bark, moist loamy banks, wet rocks, dry cliffs and ledges, roots, sandy moist soil and a multitude of other habitats but perhaps most common and successful on moist, decaying logs which it often colonizes almost to the exclusion of other species. It is perhaps the most common species of moist, rather shaded logs in the "Transition" Zone and is replaced on more sunny, exposed logs by *Jamesoniella*. On moist calcareous rocks it is occasionally replaced by *L. bidentata;* on exposed, rather calcareous banks, by *L. minor*. It has the vigor to invade all these habitats however, and frequently occurs competing with species of its own genus. Fruiting very abundantly, often in July and August, well into late October (later than "February-July" as given by Ammons).

A variable and often difficult species to determine. The presence of rounded leaf-lobes on some of the apical leaves (Pl. 10, fig. 11) and the broadly rectangular shape of the leaves, are characteristics that separate it from our other species, when well indicated; poorly developed or immature material may have all the leaves with sharp lobes however, and can often be determined only with doubt. The absence of gemmae and larger size as well as paroecious inflorescence, separate it at once from the usually dioecious *L. minor*. The less decurrent leaves are quite distinct from the more decurrent, apically gradually tapering leaves of *bidentata*.

L. MINOR Nees

Frequent. TOMPKINS CO.: McKinney's Twin Glens, *R. M. & O. M. Schuster;* Esty Glen, *Schuster;* Sixmile Creek Ravine, *Schuster;* Coy Glen, *R. M. & O. M. Schuster;* Enfield Glen, *Schuster;* Fall Creek, *Schuster;* Buttermilk Glen, *R. M. & O. M. Schuster;* Lick Brook, *Schuster;* Taughannock Gorge, *Schuster & Matthysse;* cliffs at southwest corner of Cayuga Lake, *Nanz.* STEUBEN CO.: Woodhull, *Schuster & Rader.* ONONDAGA CO.: Riegal Woods (Goodrich, 1912, p. 23). ONTARIO CO.: Briggs Gully, *Schuster.* YATES CO.: roadcut near Middlesex, *Schuster & Pendleton.* MONROE CO.: Irondequoit Bay, near Rochester, *R. M. & O. M. Schuster.* SCHUYLER CO.: Watkin's Glen, *Schuster.* CATTARAUGUS CO.: Vandalia and Nichol's Run, Limestone (Boehner 1943, p. 12).

One of the common colonizing species of denuded, rather dry, loamy or sandy-loamy, calcareous or subcalcareous banks. Much less common on neutral soils and apparently absent on acid soils. Very commonly associated with *Cephaloziella rubella* and occasionally other species of that genus with which it forms a distinct society, the *Lophocolea minor-Cephaloziella* Associule. On less distinctly calcareous soils where the lime has been largely leached out, *Lophozia bicrenata* becomes a prominent accessory species, or, rarely *Lophozia excisa* (Woodhull); on distinctly acid soils, the *L. bicrenata* entirely replaces the *Lophocolea.* Also common in crevices of moist-to-intermittently dry calcareous shales and sandstones, here associated with *Scapania mucronata, Lophozia badensis* and other calciphiles. The "calciphilous" nature of the species prohibits its occurrence on humus or other acidic soils or on decaying logs; it is here always replaced by the closely related *L. heterophylla.*

The abundant gemmae formation (Pl. 10, fig. 9) of most plants in each patch, resulting often in a dusty yellow-green appearance, characteristic of this species, differentiates it from all our other Hepaticae. It somewhat resembles *L. ventricosa* in that regard, from which it differs in the presence of amphigastria and in the less chlorophyllose, more yellow-green color of the cells.

L. BIDENTATA (L.) Dumort.

Apparently rare locally. TOMPKINS CO.: Coy Glen, *Andrews;* Varna, *Schuster;* McKinney's Twin Glens, *R. M. & O. M. Schuster.* ONONDAGA CO.: Dewitt (Goodrich 1912, p. 23); Clark Reservation near Jamesville, *Schuster & Rader.* CATTARAUGUS CO.: Beehunter Creek, Allegany State Park; Cattaraugus Creek near Gowanda; Nichols Run, Limestone; Martiny Rocks, Allegany (Boehner 1943, p. 12).

Occurring mostly on moist cliffs and ledges and on moist, loamy soil. Probably much more frequent locally than the above citations indicate, but often overlooked for *L. heterophylla.*

The delicate, hyaline appearance, whitish-green color and almost constant sterility, separate this species from *L. cuspidata.* It may occasionally be mistaken for the commoner *L. heterophylla* in the field, especially since forms of the latter may approach it in facies. It is our only *Lophocolea* with decurrent leaves that are conspicuously wider basally than apically (Pl. 10, fig. 10).

II. CHILOSCYPHUS Corda

KEY TO SPECIES

1. Leaf-cells small, mostly 16-33 μ; perianth-mouth with the lobes entire or undulate; plants rather opaque, dull or deep green 2
   2. Cells of leaf-middle mostly 16-25 (28) μ; plants aquatic, usually on stones in running water; generally dark green ..... *C. polyanthus* var. *rivularis*
   2. Cells mostly 26-33 μ; plants terrestrial; dull to brownish-green ..... *C. polyanthus* (typical)
1. Leaf-cells large, 30 x 50 μ or larger; lobes of perianth-mouth more or less dentate to spinose-dentate (Pl. 10, fig. 6) 3
   3. Aquatic or subaquatic, on submerged stones or soil; cells rather chlorophyllose, dull-green, 30-40 (45) μ; leaves rounded-quadrate, never retuse at apex ..... *C. pallescens* var. *fragilis*
   3. Terrestrial; extremely transparent, pale whitish-green, little chlorophyllose, the cells of the leaf-middle 40 x 50 μ or larger; leaves rectangular, more or less truncate or truncate-retuse at apex (Pl. 10, fig. 6) ..... *C. pallescens* (typical)

C. POLYANTHUS var. RIVULARIS (Schrad.) Nees

Rare, local. CATTARAUGUS CO.: Allegany State Park, attached to stones in running water, *Boehner* (det. Schuster).

This aquatic variant or modification of typical *polyanthus* has been generally treated as a discrete species. It differs from *polyanthus* in its occurrence, being limited to rocks or soil beneath running waters, usually of swiftly running brooks or creeks. Apparently with only a slight tolerance for calcareous conditions.

The rather small leaf-cells, aquatic habitat and the generally deeper green color, are all that separate *rivularis* from *polyanthus*. The smaller cells may be a result of the different habitat (and the reduction in cell-size may result in concentration of chloroplasts, hence deeper color).

C. POLYANTHUS (L.) Corda

Frequent. TOMPKINS CO.: near source of Sixmile Creek, *R. M. & O. M. Schuster;* Sixmile Creek Ravine, *Schuster;* Ringwood Swamp, *Schuster.* GENESEE CO.: Bergen Swamp, *Schuster & Winne,* fruiting May 3, 1946. CHEMUNG CO.: Veteran, *Schuster, Smith, Rader,* fruiting May 10, 1946; Winters Bog, fruiting May 10, 1946. CATTARAUGUS CO.: Beehunter Creek, Allegany Park (*Boehner*); Quaker Run, near creek, with *Scapania undulata, Boehner,* det. Schuster. ONTARIO CO.: near Briggs Gully, Richmond, *Schuster.* CORTLAND CO.: west of Solon, along stream-bank, grading into next, *Schuster & Winne.*

This species is most abundant in open, wet, swampy woods where it occurs on the organic substrata found there: decaying logs, stumps and humus and on exposed roots and often around the bases of the butts of trees. In dense woods the species becomes very scarce. It is therefore not to be expected to any extent in virgin forest areas but is able to persist in swampy woodlots, after repeated lumbering, long after all but other common species *(Conocephalum, Lophocolea heterophylla)* have disappeared; it is here also occasionally associated with *Geocalyx graveolans.* Apparently less able to tolerate large amounts of lime than *C. pallescens* and to some degree replaced by the latter under very marly conditions.

The relatively small size of the cells (28-33 μ) distinguishes this species from both of the next forms. Unlike the two next forms, typical *polyanthus* has the three lobes of the perianth entire or merely sinuate-undulate.

C. PALLESCENS var. FRAGILIS (Roth) Müll.

Frequent. TOMPKINS CO.: near source of Sixmile Creek, *R. M. & O. M. Schuster;* Connecticut Hill, *E. S. Ford.* LIVINGSTON CO.: Swiftly flowing sluices of Fish Hatchery at Caledonia, *Muenscher, Schuster, Winne.* CATTARAUGUS CO.: Mt. Moriah, Vandalia; Jones Hill, Steamburg (Boehner 1943, p. 12).

Occurring around ponds and in the flowering waters of streams, with a wide toleration for lime and sometimes (Caledonia) on submersed cement sluices. More often on rocks in streams or on the banks of streams. Perhaps specifically distinct from *pallescens* but all of the above sterile material differs only in cell size — a very slight and easily modified characteristic upon which to found species.

The large cells (30-40 μ in the leaf-middle), the dull, often light olive-green color and the occurrence, characterize this form. Perianths which are rarely produced, possess dentate lobes, similar to those of *pallescens* rather than to those of typical *polyanthus*.

C. PALLESCENS (Ehr.) Dumort.

Infrequent. TOMPKINS CO.: Sixmile Creek Ravine, *Schuster.* CATTARAUGUS CO.: Beehunter and Stoddard Creeks, Allegany State Park (Boehner 1943, p. 12). CAYUGA CO.: Paines Gully, *Andrews & Schuster.* ONONDAGA CO.: Clark Reservation, near Jamesville, *Schuster & Rader.* GENESEE CO.: Bergen Swamp, among mosses, *Moerkia, Riccardia pinguis, Lophozia rutheana* and other "calciphilous" Hepaticae, on thin soil impregnated with underlying marl, in *Thuya* Associes, *Schuster & Winne,* fruiting May 3, 1946.

This species occurs at times under similar conditions as *C. polyanthus* but has a wider tolerance for lime. It is one of the characteristic species of decaying humus and logs in *Thuya* swamps. Both light tolerance and lime tolerance vary widely; the species may occur under decidedly shaded-to-quite-exposed situations, it may occur on acid rotting logs or almost directly over marl. In each case, some humus or organic matter seems prerequisite. In our area I have never found it associated with rocks. Both it and *C. polyanthus* occur successionally, at first on the bark of decorticated trees (most often in swamps), usually as members of the *Cephalozia-Riccardia pinguis-R. latifrons* lociation of the *Nowellia-Jamesoniella* Associule. Neither species is ever common under conditions as exposed and mesic as those preferred by the latter group of species. They continue to play a distinct role as accessory species until the relatively uniform conditions of the forest floor is reached.

The very hyaline, nearly pellucid, whitish green color (with a slightly bluish tinge), the large cells and the frequent occurrence of truncate-retuse leaves, and near the junction of branches with main stem, distinctly emarginate leaves, characterize the sterile plant. The dentate perianth-lobes (Pl. 10, fig. 6) separate the species at once from *polyanthus,* when fertile.

Müller (1942) has critically treated our forms of this genus. He reduced the four species to two (*pallescens* and *polyanthus*) and transferred *fragilis*

from *polyanthus* (near or in which it was usually placed) to *pallescens*. His work is based on at least a minimal amount of culture of the species and on a consideration of the fact that *polyanthus* (and its variety *rivularis*) has only 9 chromosomes per cell, while *pallescens* (and its variety *fragilis*) has 18 chromosomes. Frye and Clark unfortunately follow the older (1912) work of Schiffner and do not mention the more recent treatment by Müller which appears to be based, in the writer's opinion, on a much more objective approach.

III. HARPANTHUS Nees

KEY TO SPECIES

1. Plant 0.8-1.8 cm long, less than 1.2 mm wide; leaf-sinus mostly one-fourth the leaf length deep or more, often obtusely angulate or rectangular; amphigastria often connate to leaves on one side of stem; trigones usually large ..... *H. scutatus*

1. Plant 2-8 cm long, 1.8-3 mm wide; leaf-sinus a shallow, lunate emargination less than one-sixth the leaf-length; amphigastria free; trigones usually small or none ..... *H. flotowianus*

H. FLOTOWIANUS Nees

Very rare. CATTARAUGUS CO.: "on decaying wood near water in Waterman Swamp, Napoli." (Boehner 1943, p. 12); not seen by the writer.

One of the rarest of Hepaticae in the eastern United States, known only from the above record. The present occurrence is extraordinary in that the species here is fully as much a glacial relict as is *Scapania cuspiduligera* and *subalpina*. The species occurs under nearly identical conditions as *H. scutatus* and has often been confused with it; unlike *H. scutatus* the present species also occurs among *Sphagnum* in bogs. The high elevation of Waterman Bog and the prevalence of other northern plants makes the occurrence there of this subalpine species somewhat less astounding.

The large size, generally is sufficient to differentiate this species from *H. scutatus*. The very shallow, lunate sinus of the more or less decurrent, ovate-circular leaves is highly characteristic and separates the species from all other local Hepaticae except some forms of *Lophocolea* from which it can be told at once by the large, entire, ovate amphigastria.

Further reports of this species from our region are needed to confirm the report of the species by Boehner (1943).

H. SCUTATUS (W. & M.) Spruce

Rather scarce but widespread. TOMPKINS CO.: Enfield Glen, 1893, *Wiegand;* Slaterville Swamp, *Schuster;* Sixmile Creek below Sixhundred Ravine, 1945, *Andrews & Schuster;* Coy Glen; Dusenberry Hollow, 1920, *Andrews.* CORTLAND CO.: Robbins Glen, Truxton, 1893, *Wiegand.* MADISON CO.: Cazenovia (Underwood & Cook, Hep. Amer., No. 37). ONONDAGA CO.: Jamesville, 1888, *Underwood & Cook.* CAYUGA CO.: Paines Creek near Aurora, 1945, *Schuster & Andrews.* ONTARIO CO.: Briggs Gully, Richmond, 1945, *Schuster.* CATTARAUGUS CO.: "decaying wood at Cold Spring and on Jones Hill, Steamburg" (Boehner 1943, p. 12); "on rather dry rocks, Martiny Rocks," *Boehner,* det. by Schuster. GENESEE CO.: Bergen Swamp, *Schuster & Winne.* CHENANGO CO.: Plymouth Pond (Reservoir), S. Plymouth, on rotten stump with *O. denudatum, Lophozia porphyroleuca, Scapania paludicola,* etc., *Schuster & Winne;* Bog near South Plymouth,

on rotting logs with *Riccardia palmata* and *latifrons, Blepharostoma, Lepidozia reptans* and *Jungermannia lanceolata, Schuster & Rader.* CHEMUNG CO.: Van Etten (*Barbour No. 7*).

Occurring mostly on decaying, moist, shaded logs or semi-shaded logs, generally with *Cephalozia media* and *catenulata, Lophocolea heterophylla, Nowellia, Jamesoniella* (i.e. as a characteristic member of the *Nowellia-Jamesoniella* Associule) more rarely with *A. helleriana, Riccardia latifrons,* etc. The species is mostly found in or near the ravines but has also been found in several of the swamps and bogs where it may also occur on peaty, moist soil at the edges of brooks, but such humicolous colonies are rare locally. Becoming commoner and more ubiquitous northward where it is often found on peaty thin soil over moist ledges and cliffs.

Differs from all bilobed leaved species with succubous leaves in that there are large underleaves present, lanceolate or ovate-lanceolate in form, that are often united at base to the base of a leaf; a further distinguishing characteristic appears to be the presence occasionally of many erect, attenuate, pale brownish shoots bearing gemmae. These shoots are usually considered as occurring only very rarely; in local collections they usually occur abundantly. Perhaps most easily confused with *Lophozia,* especially *L. porphyroleuca*; differing from this genus at once in the prominent underleaves.

IV. GEOCALYX Nees

G. GRAVEOLANS (Schrad.) Nees

Rather common. TOMPKINS CO.: Ringwood Swamp; Sixmile Creek; Sixhundred Ravine; Coy Glen; Enfield Glen; Lick Brook; Headwaters Swamp; Michigan Hollow Swamp; McLean Bogs; Cascadilla Ravine; Fall Creek Ravine. CAYUGA CO.: Paines Creek near Aurora. ONONDAGA CO.: Clark Reservation near Jamesville; White Lake, Jamesville; "Onondaga County," Underwood & Cook, Hep. Amer. No. 16. MADISON CO.: Chittenango Falls. YATES CO.: Middlesex. CORTLAND CO.: Virgil. GENESEE CO.: Bergen Swamp. CHEMUNG CO.: Winters Bog, in southwest corner of County; Van Etten (*Barbour No. 7*). SENECA CO.: near Junius Peat Bogs. TIOGA CO.: southern part of Headwaters Swamp. ONTARIO CO.: Briggs Gully, Richmond. CHENANGO CO.: Plymouth Pond, S. Plymouth. CATTARAUGUS CO.: Jones Hill, Steamburg; Waterman Swamp, Napoli; Ashford, etc.

Occurring most abundantly on substrata rich in organic matter, as humus, decaying wood in an advanced state of decay, rotting muck in swamps; more rarely occurring on moist loamy soil or (very rarely) on the vertical, shaded sides of moist rocks (Enfield Glen). A species limited in its tolerance of light, occurring most commonly on moist, springy banks and on wet ravine-slopes or in wet swampy woods where the arborescent covering is dense. Almost invariably to be found associated are *Trichocolea, Calypogeia neesiana, Cephalozia connivens,* etc. Occasionally occurring with *Lepidozia, Blepharostoma* and *Jungermannia lanceolata.* Apparently not "calciphobous," and limited in distribution to subcalcareous or slightly acid substrata; in the ravines occasionally occurring under somewhat calcareous conditions.

The peculiarly opaque, yellow to bright-green color of the plants is characteristic; when once appreciated, this character will be alone sufficient to identify the species. It differs from all bilobed-leaved Hepaticae of our area

in that large underleaves are present, which are bifid nearly to base, with the linear segment not provided with lateral teeth (Pl. 10, fig. 12). The constant absence of perianths (but usually with the cylindrical, rhizoidous, subterranean perigynia evident on careful inspection) separates it from all other forms with bilobed leaves.

Family PLAGIOCHILACEAE

I. PLAGIOCHILA Dumort.

P. ASPLENIOIDES (L.) Dumort.

Locally common. TOMPKINS CO.: Ringwood Swamp; Sixmile Creek Ravine; Headwaters Swamp; Michigan Hollow Swamp; Cascadilla Ravine; Shurger Glen; Sixhundred Ravine; Coy Glen; Enfield Glen; Buttermilk Glen; Lick Brook; Old Buttermilk Ravine; Taughannock Ravine; ravine just south of Taughannock; McKinney's Twin Glens; Fall Creek Ravine; Forest Home. TIOGA CO.: southern part of Headwaters Swamp. ONONDAGA CO.: Cicero Swamp (Goodrich 1912, p. 24); Clark Reservation near Jamesville. GENESEE CO.: Bergen Swamp. SCHUYLER CO.: Watkins Glen. MONROE CO.: Irondequoit Bay. STEUBEN CO.: near Woodhull. WAYNE CO.: Clyde (Underwood & Cook, Hep. Amer., No. 20). CHEMUNG CO.: Winters Bog. CORTLAND CO.: Kenney Creek Gulf, Truxton; Virgil. ONTARIO CO.: Briggs Gully, Richmond. CAYUGA CO.: Paines Creek near Aurora. CATTARAUGUS CO.: Gowanda; Steamburg; Cold Spring; Martiny Rocks, Allegany (Boehner 1943, p. 13).

An abundant species in the ravines where the shade and constant supply of moisture make possible large colonies of the species, often in deep, luxurious mats. With a wide tolerance for both acid and calcareous substrata, occurring on rotting logs in wet swamps (Ringwood) or directly on moist, subcalcareous sandstone (Sixmile Creek). The two chief requirements of the species appear to be abundant, rather constant moisture and absence of much direct sunlight. When growing on decaying wood in sunny swamps, it enters into association with such xylicolous forms as *Lophozia porphyroleuca*; such occurrences are decidedly unusual, however. In the ravines and in shaded swamps it usually grows with *Bazzania trilobata, Jungermannia lanceolata, Blepharostoma* and *Geocalyx*. Occasionally when growing on thin soil over calcareous shale, it forms deep mats, associated with *Reboulia*.

P. asplenioides is one of the characteristic Hepaticae of the Pine-Hemlock-Yellow Birch Ravine Slope and Bog Forest community, but occurs perhaps most abundantly on Hemlock-Mountain Maple covered slopes of ravines with exposed, moist rocks.

Since male and female plants of this dioecious species normally occur in separate patches, sporophytes are produced only rarely as at Coy Glen, April 24, 1943.

The entire leaves (in our material rarely with the fine marginal teeth at all well-developed), strongly decurrent dorsally with the dorsal leaf-margin somewhat decurved or reflexed (so that the dorsal leaf-margin is often not visible from above) are sufficient to identify this species. Determination is very easy with material that has been allowed to dry for a little while, since the degree to which the posterior leaf-margin is deflexed becomes much accentuated and the leaves curl up in a characteristic manner unlike all our other

Hepaticae, when dry. Poorly nourished, impoverished forms often may be mistaken for *Jungermannia lanceolata* or *Jamesoniella*; exact examination will reveal numerous differences, mentioned under the latter two species.

Family SCAPANIACEAE

I. DIPLOPHYLLUM Dumort.

D. APICULATUM (Evs.) Steph.

Scarce locally. TOMPKINS CO.: Lick Brook, *R. M. & O. M. Schuster;* Enfield Glen, var. *coll.;* Sixmile Creek Ravine, *Schuster;* Coy Glen, *Andrews, Schuster;* crest of Fall Creek Ravine, *R. M. & O. M. Schuster;* Taughannock Ravine, *Schuster.* CATTARAUGUS CO.: north of Rock City, *Schuster & Rader.* ONTARIO CO.: Briggs Gully, *Schuster.* ONONDAGA CO.: "Tamerac Swamp" (Goodrich 1912, p. 22, as *D. albicans* var. *taxifolium* (Wahl.) Aust.).

This species occurs only very locally but in several places (Enfield, Briggs Gully and Taughannock) it is an abundant species. The relative rarity is perhaps due largely to the absence of acid rocks which this species appears to prefer; with only a very small tolerance for lime and when occurring on shale and sandstone limited to non-calcareous outcrops. A species locally of moist clayey or loamy soils, occasionally on sandy-loamy soil; usually entirely avoiding soils rich in humus and apparently never present on decaying wood. Frequent on both exposed and denuded loamy banks or on thin soil between rocks or ledges near the crests of ravines, occasional on moist, disintegrating shale talus. Commonly associated species are *Scapania nemorosa, S. mucronata, Lophozia ventricosa, Jamesoniella autumnalis, Lophozia bicrenata, Plectocolea crenulata;* on vertical rock faces as at Enfield, *Leucolejeunea clypeata* and *Scapania nemorosa* are the commonly associated species. Rather frequent on the limited siliceous conglomerates near Rock City, again associated with *S. nemorosa.*

The record listed above from Onondaga County certainly belongs here; the var. "*taxifolium*" of Austin has been placed as a synonym of *apiculatum* by Evans; furthermore, *taxifolium* is a much more northern, montane species not to be expected in our area.

The elongate, lingulate ventral lobes (Pl. 13, fig. 12, 14) of the leaves, narrowed and apiculate at apex, directed at a decidedly different angle from the stem (usually at a 90-120 degree angle with the stem) than the dorsal lobes (which usually are much more anteriorly directed) result in what appears to be four rows of distinct leaves; this together with the locally always bright to deep green color, and the larger size as compared with *Scapania mucronata,* adequately differentiate the species. The polygonal, angulate gemmae (Pl. 13, fig. 13) separate it at once from *Scapania.*

Not reported for Cattaraugus County by Boehner (1943).

II. SCAPANIA Dumort.

The genus *Scapania* continues to occupy the attention of Hepaticologists. Buch (1922, 1928) most recently has revised the Palearctic species of the Scapaniaceae, contributing a highly critical treatment very useful to students of the Nearctic species. He divided the family into four genera (as regards

Holarctic species): *Douinia, Diplophyllum, Scapaniella* and *Scapania.* Species of the latter three groups occur in the area treated. These genera have been accepted by Evans (1939), Frye and Clark (1937-1947) and other students. However the genus *Scapaniella* has not been universally accepted, Müller (1939, 1939-1940) not accepting it at all, while Jørgensen (1934) reduced it to the status of a subgenus, with a somewhat different delimitation than given by Buch. Frye and Clark's treatment (1946) unfortunately can scarcely be followed since the differences in treatment from that in Buch represent decided regressions. Their statement that the genera are poorly isolated applies only to *Scapaniella,* and to *Scapania* and *Diplophyllum as they delimit them.* They for instance include *Sc. gymnostomophila,* a species with sharply keeled leaves and smooth, ovoid gemmae, in *Diplophyllum;* giving the latter genus limits that cannot be clearly defined from those of *Scapania.* Very unfortunately, the key to *Scapania* in Frye and Clark is unusable and leads to numerous misdeterminations.

One of the difficult points in the classification of the family is the disposition of *Sc. cuspiduligera.* This species has the perianth, leaf-form, and gemmae of *Scapania,* but the unkeeled, somewhat sheathing leaf-base of *Diplophyllum.* Buch (1928) kept the species within the subgenus *Euscapania,* a disposition that made circumscription of that subgenus virtually impossible. Jørgensen (1934) included the species in the subgenus *Scapaniella* (Buch) emend. Jørg., a disposition scarcely more fortunate than that of Buch. It would seem best, in the writer's opinion, to create a separate subgenus for this isolated species. With the segregation of *Sc. cuspiduligera* in a discrete subgenus, the classification of the genus *Scapania* becomes considerably simpler. *Scapaniella* is included within the genus *Scapania* since the chief character stressed by Buch (1928) in his key (the border of larger-celled, thick-walled marginal cells of the leaves) fails with the species *Sc. glaucocephala.* Since stem-sections are necessary in order to use this key to subgenera, an artificial one is given (p. 593) direct to species.

KEY TO SUBGENERA

1. Leaves with commissure not keeled at base, but the basal portion of the leaves curved, somewhat erect and sheathing the stem, becoming keeled only in the distal part of the commisure; leaf-margins entire or virtually, margined by 1-several rows of thick-walled cells; perianth flattened, scapaniate, with the truncate-mouth with thick-walled cells, entire; cells of gemmiparous leaf-apices very large. (Small species, 2-10 mm; gemmae brownish; plants green, unable to produce secondary pigmentation) 2

2. Oil-bodies small 3-5 μ or smaller, 5-6 per cell or more; stem with cortex of cells equal in size to inner cells, isodiametric in cross-section; leaves with acute lobes, the dorsal about half the ventral in size; ventral leaf-base non-decurrent; plants "calcifuge": only on decaying wood ..... *Scapaniella*

2. Oil-bodies very large, 6-12 μ or larger, 1-3 per cell mostly; stem with cortex of small, tangentially flattened cells, different from the medullary cells; leaves (on non-gemmiparous shoots) with broadly rounded lobes, the dorsal squarrose, subequal to ventral in size; ventral leaf-base decurrent; plants "calciphile": only on basic soil or basic rocks ..... *Buchiella* subg. n.

1. Leaves with commissure distinctly keeled to base, the basal portion of the leaves

sharply angulate, spreading, not sheathing stem; cells of gemmiparous leaf-apices normally no larger than other cells 3

3. Oil-bodies large, brownish, long-persistent in dry material, 1 per cell except in basal or gemmiparous cells; ventral leaf-lobe somewhat concave, falcate; dorsal lobe 1/3 - 1/5 the ventral in size; perianth little flattened, deeply plicate, narrowed to mouth; leaf-margins totally entire ..... (*Kaalaasia*)

3. Oil-bodies small, generally 3-many per cell, disappearing soon after death of plants; ventral leaf-lobe flat or convex, not distinctly falcate; dorsal lobe 1/3 - 3/4 the ventral in size; perianth strongly flattened, with no distinct dorsal or ventral keels, broad and truncate at mouth; leaf-margins more or less denticulate usually ..... *Euscapania*

The writer believes *Buchiella* is fully as worthy of subgeneric segregation as is *Kaalaasia*. The very large oil-bodies of *Sc. (Buchiella) cuspiduligera* have not been previously noted and are very different from those of *Scapaniella*. This together with the different stem-structure, the very different leaf-shape and other characters, suggest that Jørgensen's (1934) inclusion of *cuspiduligera* in *Scapaniella* is unnatural. In the oil-bodies *cuspiduligera* approaches *Kaalaasia*, a fact overlooked by Buch (1928) when he left *cuspiduligera* in *Euscapania*. With the segregation out of *cuspiduligera* it remains possible to sharply differentiate between *Kaalaasia* and *Euscapania*.

ARTIFICIAL KEY TO SPECIES

1. Small species (Pl. 13, fig. 1; Pl. 12, fig. 1), to about 6 mm long or less, occurring only on rotting wood; erect, slender shoots with gradually reduced leaves present, bearing reddish-brown gemmae at their apices 2

2. Leaf keeled only on outer half of commissure, the basal half evenly rounded, somewhat sheathing stem; gemmae 2-celled (Pl. 12, fig. 2), at the tips of bilobed leaves; marginal leaf-cells equally thick-walled (Pl. 12, fig. 3) ..... *S. (Scapaniella) glaucocephala*

2. Leaf keeled to base, not sheathing stem; gemmae 1-celled (Pl. 13, fig. 4), gemmiparous leaves with lobes reduced or absent; marginal leaf-cells like interior cells, thin-walled, with bulging trigones (Pl. 13, fig. 2) ..... (*S. (Scapania) apiculata*)

1. Larger species, over 8-80 mm long, only exceptionally on rotting wood (not confined to it); gemmae at apices of normal, not apically attenuate and flagelliform shoots, on unmodified leaves 3

3. Dorsal lobe ¾ or more the ventral lobe in size (Pl. 12, fig. 5); ventral lobe long-decurrent (Pl. 12, fig. 5); gemmae 2-celled (Pl. 12, fig. 6); leaves with keel mostly ½-¾ the ventral lobe in length (Pl. 12, fig. 5), very weakly arched or straight; plants pale bluish to pale yellowish-green; leaves bordered with equally thick-walled cells (Pl. 12, fig. 4) 4

4. Leaves with commissure not keeled near base, the basal part of the leaf broadly sheathing the stem (Pl. 12, fig. 5); both lobes totally entire, rounded at apex (Pl. 12, figs. 4, 5); leaf-incision ¼ the ventral lobe long, the keel very long; dorsal lobe squarrose (Pl. 12, fig. 5); to 12 mm long; gemmae brown ..... *S. (Buchiella) cuspiduligera*

4. Leaves distinctly keeled to base of commissure, not clasping stem below; leaf-lobes usually distantly dentate, pointed or obtusely angulate at apex; leaf-incision 2/5 - 1/2 the ventral lobe long, the keel moderate in length; dorsal lobe not squarrose, lying over ventral lobe; to 25 mm long; gemmae greenish ..... *S. (Scapania) subalpina*

3. Dorsal lobe not more than half the ventral in size (occasionally somewhat larger on immature leaves near stem apex) (Pl. 13, fig. 5); leaves with keel ½ or less the ventral lobe in length (Pl. 13, figs. 5, 8-11); leaves keeled to base 5

5. Ventral lobe narrow, elongate, mostly 0.5-0.8 as wide as long (Pl. 13, fig. 5), not or scarcely decurrent at base; dorsal lobe arching about half-way across the stem; small species, less than 1.5 cm long; gemmae yellow green ..... *S. (Scapania) mucronata**

5. Ventral lobe wider, 0.8-1.3 as wide as long (Pl. 13, figs. 8-11; Pl. 12, figs. 7-9); larger species, over 2 cm long; dorsal lobe frequently reaching entirely across stem, often arching somewhat beyond it (Pl. 12, figs. 8, 12; Pl. 13, figs. 8-9) 6

6. Gemmae 1-celled, cinnamon-brown (Pl. 13, fig. 7); dorsal lobe distinctly decurrent, arching far across stem (Pl. 13, figs. 8-9); leaf-lobes strongly dentate normally, the teeth spinose, of 1-3 elongate cells each (Pl. 13, figs. 8-9); neither in bogs nor submerged in streams; often reddish tinged, in part ..... *S. (Scapania) nemorosa*

6. Gemmae partly or entirely 2-celled, pale greenish to greenish-brown (Pl. 12, fig. 11); leaf-lobes entire or subentire (Pl. 12, figs. 7-9; Pl. 13, figs. 10-11), if with remote, small teeth, these consist of single isosceles-triangular cells; dorsal lobe not or scarcely decurrent (Pl. 12, figs. 9, 8; Pl. 13, fig. 11) 7

7. Keel of leaves straight or slightly arcuate (Pl. 12, fig. 9), never semi-circularly arched on any leaves, from 1/2 - 1/3 the ventral lobe in length; dorsal lobes rounded-rectangular, with the apical point obliquely outward directed at at least a 30 degree angle with the stem (Pl. 12, figs. 9, 12; Pl. 13, figs. 10-11); dorsal lobes not or little arching across stem 8

8. Ventral lobes not at all decurrent basally (at most with an inconspicuous strip a single cell wide running down a little below insertion of keel) (Pl. 12, fig. 9); leaf-lobes entire; only in swamps and bogs ..... *S. (Scapania) irrigua*

8. Ventral lobes distinctly decurrent basally, the decurrent strip extending fully for half the length of the stem-segment (Pl. 13, figs. 10-11), more than a single cell wide most of its length; leaf-lobes rounded or nearly, occasionally toothed (Pl. 13, fig. 10); near or in running water ..... *S. (Scapania) undulata*

7. Keel of leaves mostly or invariably strongly, semi-circularly arched, only 1/6 - 1/4 the ventral lobe in length (Pl. 12, figs. 7-8); dorsal lobes cordate or heart-shaped, with the point directed approximately towards the stem apex; dorsal lobes always arching far across and beyond stem (Pl. 12, figs. 7-8); ventral lobe scarcely decurrent, the decurrent strip not extending below point of insertion of keel of leaves; cells thin-walled, normally with strong, often bulging trigones; lobes more or less pointed ..... *S. (Scapania) paludicola*

Subgenus **Buchiella** Schuster, subg. n.

S. (BUCHIELLA) CUSPIDULIGERA (Nees) K. Müll.

Exceedingly rare and local. CATTARAUGUS CO.: Martiny Rocks, West Branch of the Four Mile, Allegany (Boehner 1943, p. 13); det. by Dr. W. Steere, not seen by writer.

This species has been reported but a very few times from North America, generally associated with moist, rocky calcareous ledges or banks (measured pH 6.9, 7.0) either directly on the rock faces or on thin soil, associated with such species as *Leiocolea* spp., *Jungermannia* spp. and various Lophoziae. The subalpine-to-alpine and arctic distribution of the species has been repeatedly emphasized and its occurrence here cannot be interpreted as other than as a highly relict disjunct of the glacial period, that has been isolated in one restricted pocket in the Alleghany Plateau. It may not be out of place to

* See Appendix, p. 703, for *S. curta*.

stress that the locality is in the unglaciated portion of the plateau, which barely enters Western New York. The species apparently was barely pushed south of the terminal moraine and never migrated further south.

The squarrose, reflexed, dorsal lobes, three-fourths or more the ventral in size and the unkeeled basal part of the commisure of the leaves which closely sheathes the stem, are highly characteristic (Pl. 12, fig. 5). The species differs from *S. subalpina* our only other local species with subequal leaf-lobes, in the entire leaf-margins, a much smaller maximum size (about 1 cm rather than about 3 cm) and in the narrower form of the leaf-lobes as well as in the characteristic pale, bluish-green color. The leaf-lobes are furthermore rounded (Pl. 12, fig. 4) and quite entire-margined.

Subgenus SCAPANIELLA Buch

S. (SCAPANIELLA) GLAUCOCEPHALA (Tayl.)

Very rare, local. ONONDAGA CO.: Syracuse (Underwood & Cook, Hep. Amer. No. 79); Tamerac [Swamp], on rotten log (Goodrich 1912, p. 24). CAYUGA CO.: Salmon River Ravine, near Genoa, *Andrews*. TOMPKINS CO.: Pony Hollow, headwaters of Newfield Brook, *Andrews*.

This rare species is limited in occurrence (like other members of the subgenus *Scapaniella*) to decaying decorticated logs. It is here a member of the *Nowellia-Jamesoniella* Associule, occurring generally under more mesic conditions and under conditions of lesser insolation than either *Nowellia* or *Jamesoniella*. On decaying logs commonly with *Blepharostoma, Lophozia incisa, Sc. apiculata, Tritomaria exsectiformis,* etc. The pH measurements of the substrate are about 4.6 (Minnesota material). The species is a Canadian-Hudsonian form according to the classification of Merriam and is extremely rare this far southward. It normally occurs on decaying spruce or fir logs in dense coniferous forests.

The very minute size (rarely over 36- mm long), restricted occurrence and the green color with the reddish-brown heads of gemmae in distinct contrast, give the species a distinctive facies. Likely to be mistaken only for *A. (Crossocalyx) hellerianus* which does not have complicate-bilobed leaves or for *Tritomaria* (which has many 3-lobed leaves), among local forms. The species is likely to be mistaken for *Sc. apiculata,* not yet found locally. The characters in the key will most easily separate the two species: of these, the 2-celled gemmae of *glaucocephala* and the equally thick-walled border of cells margining the leaves, are perhaps the most important.

In the opinion of the writer, *Scapaniella* Buch is not sufficiently distinct from *Scapania* Dumort. to deserve generic recognition. I therefore follow Jørgensen (1934) in treating it as a subgenus. However I cannot follow Jørgensen in including in *Scapaniella* the isolated *Sc. cuspiduligera.*

Subgenus EUSCAPANIA K. Müll., emend.

(S. (EUSCAPANIA) APICULATA Spruce

Doubtfully present in our region. Two reports of the species from Tompkins and Cayuga counties (det. by Andrews), are now to be placed in *Sc. glaucocephala, fide* An-

drews, which see. These reports were the sole basis for the inclusion of the species as a member of our flora.

The species has the same ecological requirements and restrictions as *Sc. glaucocephala* and is superficially very similar to it in size, in the production of reddish-brown gemmae on erect or ascending shoots, bearing reduced leaves, as well as in its occurrence on rotting logs. Previously reported by Peck from North Elba, New York. Since *glaucocephala* occurs in several localities in our region, *Sc. apiculata* should be looked for locally.

The most obvious differences from *glaucocephala* lie in the strongly collenchymatous leaf-cells (even the marginal have bulging trigones (Pl. 13, fig. 2) and do not form any sort of border), the totally 1-celled gemmae (Pl. 13, fig. 4) and the tendency for the leaves of the erect gemmiparous shoots to be extremely reduced, losing all indication of a sinus (in *glaucocephala* always distinctly bilobed). The other characters of the species are rather similar.

S. (SCAPANIA) MUCRONATA Buch*

Scarce. TOMPKINS CO.: Enfield Glen (*sev. coll.*); Coy Glen, *A. L. Andrews & R. M. Schuster;* Fall Creek Ravine, *R. M. Schuster;* Buttermilk Glen, *R. M. & O. M. Schuster,* Taughannock Gorge, *R. M. Schuster;* Lick Brook, *R. M. & O. M. Schuster.* STEUBEN CO.: Woodhull, *Schuster & Rader.* CHEMUNG CO.: Veteran, near Elmira, *Schuster, Rader, Smith.*

Limited in occurrence locally to somewhat moist ravine walls, where it occurs either directly on the walls, in crevices or on the moist talus at their base; occasionally on thin soil over the shale as at Fall Creek (associated with *Lophozia ventricosa, Cephaloziella hampeana*) and near Woodhull (associated with *Lophozia excisa* and *ventricosa, L. barbata*). Locally, appearing quite tolerant of calcareous conditions although Buch states the species is limited to siliceous rocks when it is epilithic. The usually associated species are *Scapania nemorosa, Diplophyllum apiculatum* and generally, *L.* (*Leicolea*) *badensis* as well as frequently, *Lophocolea bidentata* and *Lophocolea minor.* Locally it forms a definite associule of moderately moist cliff-walls, the *Scapania* Associule consisting of the above species. Associated with these are frequently *Lejeuna cavifolia* and *Radula obconica,* more rarely *Lophozia ventricosa* and *Tritomaria exsectiformis.*

The small size, usually scarcely 1.5 cm tall, the yellow-green gemmae and the stiff, entire-margined leaves with narrow ventral lobes, as well as the fact that the dorsal lobes usually only about half cross the stem, easily distinguishes this species (Pl. 13, figs. 5-6).

S. (SCAPANIA) IRRIGUA (Nees) Dumort.

Rare, local. TOMPKINS CO.: South Hill Marsh, south of Ithaca, *R. M. & O. M. Schuster.* CHENANGO CO.: Plymouth Pond (Reservoir), near S. Plymouth, and outlet of Plymouth Bog, *Schuster & Winne,* March 1946.

A northern species, occurring here around its periphery (though reported from as far south as Washington, D. C., and New Jersey). Apparently with a tolerance for small amounts of lime, preferring subcalcareous or neutral areas but often present in bogs in calcareous regions. Locally occurring on

* See Appendix, p. 703.

exposed, loamy, moist-to-wet soil of a hill-top marsh (Tompkins County), associated with *Plectocolea crenulata, Cephaloziella rubella* and *Lophozia bicrenata* as well as in less pachydermous modification among a *Sphagnum-Polytrichum* society. At the Chenango stations it occurred with *S. paludicola, Lophozia porphyroleuca* and *Odontoschisma* on wet rotting logs, as well as among *Sphagnum, Pallavicinia lyellii* and with *S. nemorosa* (at the edges of a flowing outlet of the bog). The Chenango station is of interest in that the species occurs here with *S. paludicola* yet remains perfectly distinct from it. In critical study of much material, none of which however, was of the very difficultly determinable extreme leptodermous form, no difficulty was experienced in separating the two species. Occasional individual shoots of *irrigua* had isolated leaves with strongly arched keels but in no cases were the dorsal leaf-lobes of the characteristic *paludicola* form, nor did they at all widely cross the stem. The frequent occurrence together of these two species is certain proof that they are perfectly good species.

The record of *S. undulata* from Onondaga County, by Goodrich (1912), may possibly belong here.

The habitat, the non-decurrent leaf-lobes (Pl. 12, fig. 9) with the ventral nearly or quite as wide as long, and the 2-celled, yellow-green gemmae (Pl. 12, fig. 11) are characteristic. The weakly-to-moderately arched keel of the leaves and obliquely outward directed dorsal leaf-lobes, separate the species from *paludicola;* the broader ventral lobes separate it from *mucronata.*

S. (SCAPANIA) PALUDICOLA Loeske et K. Müll.

Very local, rare. CHENANGO CO.: Among *Sphagnum* and with *S. irrigua, Cladopodiella, Lophozia porphyroleuca, Cephaloziella elachista* on wet, decayed wood, near the edges of Plymouth Lake (Reservoir); in some quantity at the open edge of the moor of Plymouth Sphagnum Bog, *Schuster, Winne, Rader.*

This record is of much interest in that it marks a new peripheral point in the range of the species and considerably extends its range. Müller (1905-1916) commented on the rarity of this species outside of the mountains. Its occurrence in Chenango County at an elevation of about 1700 feet, is therefore of much interest. Both Müller and Macvicar stress that this species occurs most frequently in calcareous bogs; at the present location the flora was essentially "calciphobous" but the underlying sandstones undoubtedly resulted in the presence of at least traces of lime; the glacial drift of this region is generally rich in lime. The occurrence of such a calciphobous species as *Pallavicinia lyellii* at the second locality indicates that very little lime occurred, however. The altitudinal range of the species is with rare exceptions, between 2800 and 6000 feet.

The large size, flaccid appearance and above all, the cordate or heart-shaped dorsal lobes with the point directed towards the stem apex (Pl. 12, fig. 8), are highly characteristic of this species. The very short keel of the leaves (not more than 1/4 the length of the ventral lobe) which is very strongly, semi-circularly arched (Pl. 12, figs. 7-8), separates the species at once from all our other local species. The little decurrent dorsal and ventral lobes and the mostly distinctly pointed leaf-lobes as well as the presence of distinct (in

the local material often slightly bulging) trigones, separate the species from the deceptively similar *S. paludosa* which may yet be found in our region.

S. (SCAPANIA) UNDULATA (L.) Dumort.

Very rare, local in our area. ONONDAGA CO.: Onondaga Hill (Goodrich 1912, p. 24). CATTARAUGUS CO.: Jones Hill, Steamburg, growing on stones in a creek (Boehner 1943, p. 13); Quaker Run, on soil near creek, with *Chiloscyphus polyanthus, Boehner* (det. Schuster).

The rarity of this species is directly proportional to the abundance of calcareous or subcalcareous rocks and soils. In our region it occurs only exceptionally and appears to be entirely absent from central New York and all of the Ontario-Erie Plain. The species occurs usually on wet cliffs and ledges, on rocks in streams and brooks, occasionally on wet soil along the edges of ponds or streams.

The more or less rounded dorsal and ventral leaf-lobes with teeth absent or fine and the strongly decurrent ventral lobes, are characteristic (Pl. 13, figs. 10-11). The species differs from our other species with 2-celled gemmae by the following combination of characters: keel less than ½ the leaf-length, straight or scarcely arched; cells thin-walled with no or only minute trigones; keel of leaves distinct to leaf-base; dorsal lobe about half the ventral in size. The generally green leaves contrasted to the dark brown or black stems and the round lobes of the undulate, flaccid leaves, are diagnostic field characters. Terrestrial forms may have the leaves rather distinctly dentate; they can be separated from *nemorosa* by the 2-celled gemmae.

S. (SCAPANIA) SUBALPINA (Nees) Dumort.

Very rare, limited apparently to the northern tip of the unglaciated portion of the Allegheny Plateau in our region. CATTARAUGUS CO.: Martiny Rocks, West Branch of the Four Mile Road, Allegany (Boehner 1943, p. 13), det. by Dr. W. Steere.

The occurrence in our region of this species is as remarkable as the local occurrence of *S. cuspiduligera;* both species are essentially Hudsonian-Alpine in distribution. Undoubtedly, it occurs locally as a highly restricted relic which during the glacial period was forced south into the unglaciated part of the northern fourth of the Alleghany Plateau and died out there in all but a very limited region. Its occurrence much further south in the Alleghany Plateau is highly improbable.

The rounded, usually slightly dentate, subequal leaf-lobes with the dorsal similar in form and dentition to the ventral, are highly characteristic and serve to identify the species. The pale-to-yellow green color, larger size (to 3 cm or more) and entirely keeled leaf-commissure, are enough to separate it from *S. cuspiduligera* which also has subequal leaf-lobes.

S. (SCAPANIA) NEMOROSA (L.) Dumort.

Frequent, locally abundant, widespread on the Alleghany Plateau. TOMPKINS CO.: Sixmile Creek Ravine, *R. M. & O. M. Schuster;* Sixhundred Ravine, *R. M. & O. M. Schuster;* Crest of Fall Creek Ravine, *Schuster;* Lick Brook, *R. M. & O. M. Schuster;* McKinney's Twin Glens, *R. M. & O. M. Schuster;* Coy Glen, *var. coll.;* Enfield Glen, *var. coll.;* Taughannock Gorge, *Andrews, Schuster;* Witham's Glen; swampy area 3 miles

south of Dryden and wet bank between Dryden and Ringwood, *R. M. & O. M. Schuster.* CATTARAUGUS CO.: north of Olean Rock City, *Schuster & Rader;* "moist soil and rocks . . . St. Bonaventure; Martiny Rocks, West Branch of the Four Mile, Allegany; South Branch of Cattaraugus Creek, Gowanda; Falls of Connoisarauly Creek; and generally throughout the County." (Boehner 1943, p. 13). CHENANGO CO.: along edge of outlet of Plymouth Bog, near S. Plymouth, *Schuster & Winne.* CORTLAND CO.: Homer Gulf, Homer, *Wiegand.* STEUBEN CO.: near Woodhull, *Schuster & Rader.* ONONDAGA CO.: "Tamarac" (Swamp) (Goodrich 1912, p. 24). MADISON CO.: Cazenovia (Underwood & Cook, Hep. Amer., No. 19). ONTARIO CO.: Seneca Point, Canadaigua Lake; Briggs Gully, Richmond, *Schuster.* CHEMUNG CO.: Veteran, *Schuster, Rader, Smith.*

Widespread under a great variety of conditions but occurring most commonly associated with ravines and ledges where the humidity is high and there is a rather constant water supply. Occasionally chasmophytic, occurring on thin soil at the crests of ravines; more often growing directly on rock or scattered among other Hepaticae and mosses inhabiting vertical rock faces where moisture conditions are rather constant. With a rather wide tolerance for lime but an indifferent species that cannot be classed as a "calciphile"; equally able to thrive on strongly calcareous and entirely non-calcareous rocks. The species is quite local in occurrence but is widespread. I have found it occasionally on rotting logs near Dryden, and just below Sixhundred Ravine, and in Lick Brook. At Sixmile Creek it occurs in woods along the edges of a loamy, moist path. At most other localities it is confined either to the ravine-walls or the talus beneath or to the crests of the ravines. Commonly associated with *S. mucronata, Diplophyllum, Cephaloziella hampeana, Lophocolea minor,* etc. When invading rotten wood, associated with *Cephalozia media, C. catenulata, Nowellia* and *L. heterophylla.* On moist talus growing with *Gymnocolea inflata* and *Cephalozia biscuspidata.* The ubiquitous nature of the species and wide tolerance of conditions of both light and moisture as well as chemical and physical difference of the substratum, make this the dominant species of *Scapania* in our area, as it is almost everywhere.

The dentate leaf-margins (Pl. 13, fig. 9) together with the invariable occurrence of 1-celled, cinnamon-brown gemmae (Pl. 13, fig. 7), are sufficient to separate this species; poorly developed material is occasionally entire-margined; some of the constantly cinnamon-colored gemmae can usually be found, however. Unlike in the *undulata-subalpina* complex (which has more or less dentate leaves), the marginal leaf-cells have distinct, often bulging trigones.

Family PORELLACEAE

I. PORELLA (Dill.) Lindb.

KEY TO SPECIES

1. Ventral lobes broadly ovate to oblong, wider than the stem, more or less imbricate; xerophytes; underleaves decurrent 2

2. Ventral lobes about as wide as underleaves, broadly rounded apically (Pl. 14, fig. 5); dorsal lobes as wide as long, crispate basally; robust, irregularly pinnate; perianth-mouth with cilia dense, crowded; elaters generally unispiral ..... *P. platyphylloidea*

2. Ventral lobes narrower than underleaves, somewhat tapering towards apex; dorsal lobes of leaves of main stem ovate, longer than wide, not or scarcely crispate

basally; more slender, regularly bipinnate plants; perianth-mouth with scattered cilia; elaters all bispiral ..... *P. platyphylla*

1. Ventral lobes slender, lingulate to narrow-oblong, small, distant, narrower than the stem; underleaves small, scarcely wider than stem, not decurrent; hygrophytic, growing in places subject to inundation ..... *P. pinnata*

P. PLATYPHYLLOIDEA (Schwein.) Lindb.

Frequent, locally common. TOMPKINS Co.: Sizmile Creek; Sixhundred Ravine; Fall Creek, near Forest Home; Enfield Glen, Buttermilk Glen; Ithaca Flats; Cayuga Heights; Coy Glen; Shurger's Glen; Taughannock Glen; Esty Glen; Fern Dale; Lick Brook; northern part of Headwaters Swamp. CORTLAND Co.: Homer Gulf, Homer; Truxton; e. of Solon; Virgil. MONROE Co.: Bergen Swamp. TIOGA Co.: Headwaters Swamp near W. Danby; Summit Marsh. ONTARIO Co.: Briggs Gully, Richmond. CHENANGO Co.: Swampy woods along outlet of Plymouth Bog, S. Plymouth, *Schuster & Winne*. CATTARAUGUS Co.: "Collected everywhere in our County range." (Boehner 1943, p. 14).

Widely distributed, mostly on bark of deciduous trees but occasionally also on rather dry rocks. On bark, a member of the typical *Frullania-Radula* Associule of deciduous trees, associated with *Frullania eboracensis, F. asagrayana, Radula complanata* and *Lejeunea cavifolia*, more rarely with *Cololejeuna biddlecomiae* and *F. brittoniae*. On rocks associated usually with *Radula complanata* and *Frullania asagrayana*.

Very difficult to distinguish when sterile, from *P. platyphylla* with which it has been almost universally confused in the past. The relatively wide ventral lobes (Pl. 14, fig. 5) offer an easy, even if not absolutely constant, means of separating the two species when sterile. *P. platyphylloidea* furthermore has the base of the dorsal lobes near their posterior margin, more or less strongly crispate and undulate while it is typically plane in *platyphylla*.

P. PLATYPHYLLA (L.) Lindb.

Scarce or rare. CORTLAND Co.: between Solon and Freetown, *Schuster & Winne*. ONONDAGA Co.: Syracuse (Underwood & Cook). MADISON Co.: Chittenango Falls, *H. Wheeler* (not examined by writer). CATTARAUGUS Co.: near Four Mile Road, Allegany (Boehner 1943, p. 14).

Numerous other specimens and records of this species exist from our region; all of those that I have had opportunity to check, belong either to indeterminable material or to the above, more common species. As far as known the species occurs under identical conditions as *platyphylloidea*, i.e., as a xerophytic (rarely meso-xerophytic) corticolous or epipetric member of the *Frullania-Radula* Associule of rather exposed bark or vertical cliffs. Relatively rarely both this and the above species may occur on the exposed roots of trees.

Superficially similar to *P. platyphylloidea* but normally smaller and narrower, more regularly, pinnately branched. The leaves are not crispate at base, the ventral lobes are distinctly narrower than the underleaves and the elaters are completely bispiral. Sterile material especially of male plants, can often not be determined with certainty.

P. PINNATA L.

Infrequent. TOMPKINS CO.: Pony Hollow, Upper Newfield Creek, *Andrews;* Mud Creek near Freeville, *Andrews & Winne.* CATTARAUGUS CO.: Quaker Run, Rice Brook, and Big Basin Trail, all in Allegany State Park (Boehner 1943, p. 13). SCHUYLER CO.: Outlet of Cayuta Lake, *Pratt.* ONONDAGA CO.: Onondaga Hill (Goodrich 1912, p. 24). ONEIDA CO.: Stone in Each Branch, Fish Creek Gorge, *Winne & Muenscher.* MADISON CO.: on immersed log in cold outlet of pond, Petersborough Swamp, *Winne & Muenscher.*

This species is limited in occurrence to streams and creeks where it is either virtually always submersed or is subject to frequent inundation; apparently limited to swiftly flowing waters. Rare or absent in most of the ravines of the region but becoming more frequent in the more level creeks and small streams; with at least a moderate tolerance for lime but perhaps absent from the ravine area because of too calcareous conditions.

The habitat alone is enough to identify the species. Confusion is possible only with *Chiloscyphus pallescens* var. *fragilis.* The latter is not as dark green, does not usually become blackish in drying and has simple leaves. The ventral lobe of *P. pinnata* is small, and may be overlooked, in which case the species may be confused in the field with *Chiloscyphus.*

Family RADULACEAE

I. RADULA Dumort.

KEY TO SPECIES

1. Plants 2-3 pinnate, with bronzed or brownish, falcate dorsal lobes that neither produce gemmae nor are caducuos; trigones mostly distinct, sometimes bulging; dioecious; perianths never present ..... *R. tenax*

1. Plants 1-2 pinnate, relatively loosely, irregularly branched, green or yellow-green, with rounded or ovate dorsal lobes (Pl. 14, fig. 4); dorsal lobes caducous or gemmae present; trigones absent or indistinct; monoecious, perianths frequently produced.

   2. Gemmae present on leaf-margins; dorsal lobes never caducous; leaves densely imbricate ..... *R. complanata*

   2. Gemmae absent; dorsal lobes often caducous; leaves distant to subimbricate ..... *R. obconica*

R. TENAX Lindb.

Very rare locally. TOMPKINS CO.: Sixhundred Ravine, *A. L. Andrews, R. M. Schuster;* Dusenberry Hollow, above Sixhundred Ravine, *A. L. Andrews.*

Locally found only as a few colonies, several rather extensive with a 50-70% coverage, occurring on perpetually moist, rather densely shaded rocks, associated with *Metzgeria conjugata* and *R. obconica* forming a distinct associule. Under conditions of greater exposure and less moisture, *R. complanata* and *Lejeunea cavifolia* make their appearance and eventually replace the present associule when conditions become sufficiently xeric. The locally relatively low humidity prevents invasion of bark.

The regularly pinnate habit, the brownish color and the distant falcate leaves as well as the absence of any evident means of reproduction, characterize this species.

R. OBCONICA Sull.

Rather rare. TOMPKINS Co.: Sixhundred Ravine, *R. M. Schuster, A. L. Andrews;* Enfield Glen, *var. coll.;* Coy Glen *var. coll.;* Buttermilk Ravine, *R. M. & O. M. Schuster.* CATTARAUGUS Co.: *Boehner,* det. Schuster.

Locally limited to similar conditions as *R. tenax* but not as closely limited to shaded, protected regions; occurring also on relatively sunny cliff-walls, if the moisture is sufficient. Often growing associated with *Lejeunea cavifolia* especially when growing near the xeric limits of the species. At Coy Glen the species has been found on the bark of rotten logs.

The caducous leaf-lobes, often resulting in large areas of the older portions of the stem with only ragged basal remnants of leaves present, are sufficient to characterize this species; the duller or deeper green color and the absence of gemmae further distinguish it from *R. complanata.*

R. COMPLANATA (L.) Dumort.

Common locally. TIOGA Co.: Two miles e. of Caroline. TOMPKINS Co.: Michigan Hollow Swamp; Woodwardia Bog; McLean Bogs; Fall Creek; Beebe Lake; Sixmile Creek; Sixhundred Ravine; Lick Brook; Enfield Glen; Taughannnck Ravine; Swamp e. of Slaterville; Coy Glen; Buttermilk Glen; Old Buttermilk Glen; Cascadilla Glen. CORTLAND Co.: Homer Gulf, Homer; swampy valley e. of Solon; Virgil. SCHUYLER Co.: Watkins Glen. GENESEE Co.: Bergen Swamp. MADISON Co.: Chittenango Falls. ONONDAGA Co.: Clark Reservation, near Jamesville; Onondaga Hill (Goodrich 1912, p. 24). Syracuse (Underwood & Cook, Hep. Amer. No. 10). STEUBEN Co.: Ledges near Woodhull. ONTARIO Co.: near Briggs Gully, Richmond. ERIE Co.: Buffalo and vicinity, general (Day, p. 166). CATTARAUGUS Co.: "frequent" (Boehner 1943, p. 14).

Occurring throughout almost all of central and western New York both on bark and on the vertical faces of moderately dry rocks. Associated in both habitats with *Porella platyphylloidea, Lejeunea cavifolia* and *Cololejeunea biddlecomiae;* on bark also frequently associated with *Frullania eboracensis* which only rarely occurs with it on cliff-walls, and with *F. asagrayana* and *F. brittoniae.* Rarely as at Sixmile Creek, on roots, and spreading slightly to the soil near-by. With a wide tolerance as regards nature of the substratum, occurring also rarely on rotting wood (McLean Bogs) but present only rarely under conditons as mesic as those under which *R. tenax* and *R. obconica* occur. Much more tolerant of direct sunlight than our two other species of *Radula,* especially moreso than *R. tenax.*

All three of our species have a wide pH tolerance, occurring freely on calcareous cliff-walls as well as on bark (our other two species however, occur on bark only in areas of greater rainfall and higher humidity).

Family LEJEUNEACEAE

I. LEJEUNEA Libert

L. CAVIFOLIA (Ehrh.) Lindb.

Frequent to common locally. TOMPKINS Co.: Lick Brook; Enfield Glen; McKinney's Twin Glens; Renwick Brook; Coy Glen; Buttermilk Glen; Old Buttermilk Glen; Sixmile Creek; Sixhundred Ravine; Fall Creek near Forest Home; Taughannock Glen. CORTLAND Co.: Robbins Glen, Truxton. ONONDAGA Co.: Clark Reservation, near Jamesville; East Syracuse (Goodrich 1912, p. 23, as *L. serpyllifolia*). MADISON Co.: Chittenango Falls. SCHUYLER Co.: Watkins Glen. STEUBEN Co.: ledges near Woodhull. ALLEGANY Co.:

Centerville (Underwood & Cook, Hep. Amer. No. 8, as *L. serpyllifolia* var. *Americana*). ONTARIO Co.: Briggs Gully, Richmond. CATTARAUGUS Co.: on bark, South Branch of Cattaraugus Creek, Gowanda; Conewango Swamp, Leon (Boehner 1943, p. 14). GENESEE Co.: Bergen, Thuya bark.

Limited in the local region almost entirely to the ravines, much moreso than *R. complanata.* Evidently so, because the species is more limited to relatively humid areas; invading bark relatively rarely and usually only near ravines; apparently the bark populations locally are not or scarcely self-sustaining, the colonies of the ravine-walls serving as a reservoir. Under conditions of decided alkalinity, it may invade marly ground as at Sixmile Creek where it grows with *Mcerkia* and *Riccardia pinguis* — certainly an unusual habitat for a Lejeuneaceous plant. Occurs on bark in Enfield, Coy Glen, Fall Creek, Sixmile Creek (there also on moist roots with *Metzgeria conjugata*), Taughannock and Buttermilk Glen; in all of these, more common on moderately dry to somewhat moist ravine-walls, there associated with such species as *Scapania mucronata, Leiocolea badensis, Cololejeunea biddlecomiae* and *Leucolejeunea clypeata,* more rarely with the more moisture-loving *Metzgeria conjugata.* Rarely on bark in swamps (Bergen).

The moderately small size (larger than the minute *Cololejeunea* and decidedly smaller than *Radula* and *Leucolejeunea*), yellow-green color and bilobed underleaves, distinguish this species (Pl. 14, fig. 7). The relatively small ventral lobules (compared to the size of the dorsal leaf-lobe) and the broader, less deeply divided underleaves as well as imbricate leaves, distinguish it from the tiny *Microlejeunea.*

II. MICROLEJEUNEA (Spruce) Jack & Steph.

M. ULICINA (Tayl.) Evans

Very rare, probably often overlooked because of the minute size. TOMPKINS Co.: Coy Glen Ravine, *A. L. Andrews;* Lick Brook Ravine, on bark of *Ulmus,* April 1946, *R. M. Schuster.*

This minute species is limited to bark in our region. The limited collections and its general distribution indicate that the species needs a relatively high atmospheric humidity and does not tolerate such extremes of light as does *Frullania* or *Porella.* In both of the known localities of our area, it occurs deep in a shaded ravine where the humidity is high and the temperature relatively low. Its limitation to ravines is certainly not due to preference for low temperatures but to its xero-mesophilous preferendum (rather than xerophilous preferences). It is of interest that at the Lick Brook locality it was associated with *Metzgeria furcata* var. *ulvula,* another xero-mesophile. Both species apparently are unable to succeed locally on calcareous or subcalcareous rocks and hence do not grow on the local shales and sandstones.

The minute size (usually less than 4-5 mm long), habit of growing intertwined among other corticolous Hepaticae and mosses and the distinct, very strongly inflated leaves (Pl. 14, figs. 1, 2), are characteristic. None of our Hepaticae are as small; none of the related forms have the ventral lobes more than a fourth as large as the dorsal whereas they are half to two-thirds as large in the present form. Confusion is perhaps most likely with *Cololejeunea*

which almost approaches it in minuteness; that species has small ventral lobes, lacks amphigastria entirely and has a tuberculate cuticle.

III. LEUCOLEJEUNEA Evans

L. CLYPEATA (Schwein.) Evans

Rare. TOMPKINS CO.: Enfield Glen, *A. L. Andrews; R. M. Schuster;* McKinney's Twin Glens.

This species is locally limited to moderately dry, rather shaded calcareous and non-calcareous shale cliffs. It occurs commonly with *Diplophyllum apiculatum* at Enfield Glen.

The pale-green, often roughly circular patches and the large size (scarcely smaller than *R. complanata*), make its recognition easy. It is most likely to be mistaken for *R. complanata* from which, as well as from all other local Hepaticae, it differs in the prominent circular underleaves (Pl. 14, fig. 6).

IV. COLOLEJEUNEA (Spruce) Schiffn.

C. BIDDLECOMIAE (Aust.) Evans

Frequent locally. TOMPKINS CO.: Fall Creek near Varna, *R. M. & O. M. Schuster;* Sixmile Creek, *R. M. & O. M. Schuster;* Sixhundred Ravine, *R. M. & O. M. Schuster;* Lick Brook, *R. M. & O. M. Schuster;* Coy Glen, *var. coll.,* Cascadilla Glen, *Wiegand;* Buttermilk Glen, *Schuster;* Enfield Glen, *var. coll.;* Cayuga Lake, west shore, *Nanz;* Old Buttermilk Glen, *R. M. & O. M. Schuster;* McKinney's Twin Glens, *R. M. & O. M. Schuster.* CORTLAND CO.: Homer Gulf, Homer, *Wiegand.* ONONDAGA CO.: Clark Reservation near Jamesville, *R. M. Schuster & W. Rader;* Green Lake (Goodrich 1912, p. 23, as *Lejeunea calacrea*); SCHUYLER CO.: Watkins Glen, *Schuster.* MADISON CO.: Chittenango Falls, *R. M. & O. M. Schuster.* CAYUGA CO.: Paines Creek, *Schuster, Andrews.* TIOGA CO.: Rock along stream, two miles n.e. of Caroline, *Schuster.*

Growing almost indiscriminately on both shaded to moderately exposed, rather dry to moderately moist calcareous shale cliffs, more commonly on calcareous sandstone rocks lying loose in the ravine-bottoms and in woods on the slopes of ravines and also on the bark and roots of both deciduous and coniferous trees. The usual habitat of this species in the ravines is on moderately dry calcareous sandstone rocks (often fossiliferous) which it covers with a fine, yellow-green overcast. The species is relatively scarce directly on ravine-walls but occurs often on bark (as with *Lejeunea cavifolia* exclusively on trees only in or near ravines). Here again we appear to have a species that is dependent on a reservoir on calcareous rocks to support invasions of bark of trees, which vary from Yellow Birch to Hemlock. The light tolerance is not very great, the lower extreme occurring on hemlock bark where shade is dense because of the overlying branches, or when growing on rocks on slopes where there is a very little direct sunlight during part of the day. Moisture requirements are very moderate, the species is xerophytic to scarcely mesophytic.

The leaves with their papillose-projecting cells, at once separate this hepatic from all others; the absence of underleaves is also to be noted (Pl. 14, fig. 10).

Family FRULLANIACEAE

I. JUBULA Dumort.

J. PENNSYLVANICA (Steph.) Evans

Very rare. TOMPKINS Co.: Enfield Glen, on moist rocks, *A. L. Andrews*. CATTARAUGUS Co.: on rock in Stoddard Creek, Allegany State Park, with *Metzgeria conjugata* (Boehner 1943, p. 14).

The single record of this species indicates it to be one of the rarities in the Cayuga Lake Basin as well as of all of central New York; the explanation for its absence in the ravines probably lies in the "calciphobous" nature of the species since the abundance of shaded, moist rocks would appear to be ideal otherwise as a habitat for the species.

The habitat (wet, shaded rocks) and the dark green color as well as the pointed dorsal lobes (Pl. 14, fig. 8) and small helmet-like ventral lobes free of the stem, easily separate this distinct hepatic.

II. FRULLANIA Raddi[28]

KEY TO SPECIES

1. Dorsal lobe of leaves with distinct ocelli (discolored, darker, and usually larger cells), in a row or more or less scattered (Pl. 14, fig. 3); lobule decidedly longer than wide (Pl. 14, fig. 3); perianth smooth, simply trigonous; dioecious 2
   2. Ocelli in a sharply defined row, forming a "vein," with none scattered (Pl. 14, fig. 3); leaf-lobes rounded apically; amphigastria, if auriculate at base, never with them crispate ..... *F. asagrayana*
   2. Ocelli in a more or less regular or irregular row, but in addition often with scattered ocelli (especially in distal portion of leaf); leaf-lobes distinctly pointed; amphigastria auriculate at base, the auricles crispate ..... *F. tamarisci*
1. Dorsal lobe of leaves lacking all trace of ocelli, no "vein" (Pl. 14, fig. 9); if lobule elongate, plant autoecious and no trace of ocelli 3
   3. Lobule decidedly less than half the size of the dorsal lobe; if autoecious the underleaves cordate or lobule elongate 4
      4. Lobule considerably longer than broad; perianth simply trigonous and smooth; autoecious; bracts and bracteole entire or nearly so; underleaves not cordate at base ..... (*F. kunzei*)
      4. Lobule about as broad as long; dioecious (or underleaves cordate) 5
         5. Underleaves not cordate at base (Pl. 14, fig. 9); dioecious; perianth triangular or trapezoidal in cross-section, usually with at least a trace of tubercles and/or supplementary ridges (Pl. 14, fig. 9) 6
            6. Lobule usually explanate; mostly deep green; leaves not squarrose ..... *F. inflata*
            6. Lobule usually distinctly inflated and forming a sac, not explanate (Pl. 14, fig. 9); generally reddish-brown 7

28 This genus badly needs study in our region. Goodrich (1912) reports *F. squarrosa* from Onondaga County; this record very much needs confirmation. Boehner (1943) reports *F. kunzei*, a subtropical and lower austral species, from Cattaraugus County; this record is an error for *F. oakesiana*. The writer here records *F. inflata* from this area on the basis of material that cannot be placed with absolute certainty. Boehner (1943) reports *F. tamarisci*, a rare northern species from Cattaraugus County; this record needs confirmation. *Frullania plana* is included in the key since it was reported from Sand Lake, N. Y. by Peck, and is known from western Pennsylvania, so shall almost certainly be found here eventually. Only 3 species (*eboracensis, asagrayana,* and *brittoniae*) have been repeatedly found; before finally admitting the others cited above, further stations, of typical material must be discovered.

7. Leaves strongly squarrose when moist, densely imbricate (closely appressed to stem when dry) ..... *F. squarrosa*

7. Leaves neither squarrose when moist, nor closely appressed to stem when dry 8

8. Underleaves with the lobes entire or obscurely unidentate on sides; perianth usually with a short, broad beak, with or without tubercles (Pl. 14, fig. 9) ..... *F. eboracensis*

8. Underleaves with the lobes provided with a distinct lateral tooth on outer sides; perianth with a long, slender beak, strongly tuberculate ..... *F. brittoniae*

5. Underleaves cordate at base; autoecious; perianth simply trigonous and smooth; on shaded rocks ..... (*F. plana*)

3. Lobule very large, more than half the size of lobe, as wide as long; autoecious: the androecia short compact and nearly circular; underleaves not cordate; plants very small, reddish to purplish-brown ..... *F. oakesiana*

F. TAMARISCI (L.) Dumort.

Very rare. CATTARAUGUS CO.: "in Waterman Swamp, Napoli, N. Y., growing on a tree trunk." (Boehner 1943, p. 14); det. by L. Clark. A second collection, labelled on Maple tree, Waterman Swamp, Napoli, Nov. 12, 1940, *Boehner*, det by W. Steere, has been seen by the writer. In addition another collection is before me, labelled Entirely covering tree-trunk, Quaker Run, Alleghany State Park, *Boehner*, det. by Boehner, which is very close to the Waterman Swamp material. ONTARIO CO.: Briggs Gully, Richmond, on crest of cliff, over shale, *Schuster*.

This species has a very scattered and limited, perhaps disjunct distribution, especially south of northeastern Canada. It occurs under conditions identical to those preferred by *F. asagrayana* and is perhaps only subspecifically distinct from the latter.

The line of ocelli is shared with *F. asagrayana*, as well as the relatively slender, distinctly higher than broad, lobule. The present species differs from *asagrayana* chiefly in that the dorsal lobe is distinctly, often acutely pointed. In the present species the line of ocelli is often vaguely defined and the ocelli especially in the upper portion of the leaves, may be quite scattered; this difference is bridged, however, by considerable variation inherent in *tamarisci*.

I have compared the three above collections with more typical material of *tamarisci* from Europe as well as typical *asagrayana* (from Minnesota) and find it is not identical with either. The material has the distinctly reflexed underleaf-margins, and occasionally more or less auriculate and crisped bases of the underleaves, and has the leaf-lobes distinctly pointed, with occasional ones terminated by 2-3 single cells in a row; it therefore approaches European *tamarisci*. The chief difference in which this American material differs from European *tamarisci* lies in the somewhat smaller underleaves which are more obovate in shape (less broad below) and are less parallel-sided. In the rather less obvious underleaves it agrees with more typical *asagrayana*. The latter however, most often has the underleaf plane, or with the margins only extremely slightly reflexed near the tips.

The material from Quaker Run is very robust and approaches the var. *robusta* Lindb.

It is questionable in my mind, whether *asagrayana* should be specifically

separated from *tamarisci*. I have before me English specimens of *F. tamarisci Schiffneri* (Nicholson), leg. Nicholson, which are characterized by broadly rounded dorsal lobes; similarly, *F. tamarisci* var. *mediterranea* De Not. has rounded dorsal lobes These plants are fully as distinct from typical *tamarisci* as is *asagrayana*. Of even greater importance, the degree to which the dorsal lobes are acute is very variable in American *tamarisci*. Some of the material here listed under *asagrayana* is on the borderline and the two "species" seem to merge gradually in this as well as all other characters.

F. ASAGRAYANA Mont.

Infrequent. TOMPKINS CO.: Coy Glen, on bark of birch and on rocks, *var. coll.;* Fall Creek, *Wiegand,* 1894; Cascadilla Glen, *Wiegand,* 1893; Enfield Glen, on hemlock bark, and on rocks; McKinney's Glen, *Wiegand,* 1894; Headwaters Swamp, on birch bark, *R. M. & O. M. Schuster;* Buttermilk Glen, *Atkinson,* 1893; Sixmile Creek, on shaded, moist cliffs, *R. M. & O. M. Schuster.* TIOGA CO.: Southern part of Headwaters Swamp, on birch bark, *R. M. & O. M. Schuster.* ONONDAGA CO.: Hopper's Glen (Goodrich 1912, p. 22); Syracuse (Underwood & Cook, Hep. Amer. No. 7, as *F. grayana*). STEUBEN CO.: Ledges east of Woodhull, on calcareous sandstone, *R. M. Schuster & W. Rader.* GENESEE CO.: Bergen Swamp. CHENANGO CO.: bark of yellow birch at edge of Plymouth Bog, S. Plymouth, *Schuster & Rader.* CATTARAUGUS CO.: Stoddard Creek, Allegany Park; Waterman Swamp, Napoli. SENECA CO.: Junius Bog, on bark of *Ulmus americana, Muenscher & Brown.*

Locally the only species of the genus occurring frequently on rocks; the tolerance for lime apparently moderate, at least. Not nearly as abundant as *F. eboracensis* which apparently replaces it largely on bark other than that of birch and hemlock in the Transition Zone. Commonly associated on rocks with *Porella platyphylloidea,* on bark with other species of *Frullania* and *Porella,* more rarely as at Headwaters Swamp, with poorly developed, atypical material of *Bazzania trilobata* and *Ptilidium pulcherrimum.* Apparently a less decided xerophyte locally than our other common *Frullaniae.*

The line of more strongly pigmented cells running through the basal ⅔ of the dorsal lobe (Pl. 14, fig. 3), separates this species from all other local Hepaticae except the related *F. tamarisci,* which see.

(F. SQUARROSA (R. Bl. & Nees) Dumort.

Very rare. ONONDAGA CO.: Edward's Falls (Goodrich 1912, p. 22); this record is open to serious question: the species has not been found elsewhere this far northward.

Not separable with ease from *F. eboracensis* when dry; when moist, the much more squarrose leaves are distinctive.)

F. EBORACENSIS Gottsche

Abundant and widespread. TOMPKINS CO.: Fall Creek; Coy Glen; Buttermilk Glen; Enfield Glen; Sixmile Creek Ravine; Old Buttermilk Glen; Forest Home; Lick Brook; Taughannock Gorge; McLean Bogs; Ringwood; McGowan Wood's, near Varna; Pony Hollow near Newfield; Beebe Lake near Forest Home; southwest corner of Cayuga Lake; South Hill; Sixhundred Ravine; Ringwood Swamp; Woodwardia Bog. CHENANGO CO.: Plymouth Pond and vicinity, S. Plymouth. CATTARAUGUS CO.: "common" (*Boehmer*). CORTLAND CO.: Virgil; east and west of Solon. SENECA CO.: near Junius Bogs. TIOGA CO.: Headwaters Swamp. MADISON CO.: Chittenango Falls. ONTARIO CO.: Farmington; Briggs Gully, Richmond. ONONDAGA CO.: Syracuse (Underwood & Cook, Hep. Amer., No. 27); Edward's Falls & Hopper Glen (Goodrich 1912, p. 22); Clark Reser-

vation near Jamesville. GENESEE CO.: Bergen Swamp. STEUBEN CO.: rocks, on ledges near Woodhull. ALLEGANY CO.: near Alma. ERIE CO.: Buffalo and vic. (Day 1882, p. 166).

The dominant species of *Frullania* locally, ninety-five percent of all material seen being this species. Occurring locally almost exclusively on bark of deciduous trees; rarely, as at Sixmile Creek growing on moist rocks. Commonly associated with *P. platyphylloidea, Radula complanata* and other members of the *Frullania-Radula* Associule of dry bark; very rarely, as at Sixmile Creek, growing on dry, decorticated logs in open woods.

F. BRITTONIAE Evans

Infrequent. ONONDAGA CO.: Marcellus (Underwood & Cook, Hep. Amer. No. 48, as *F. dilatata*). TOMPKINS CO.: Enfield Glen, *var. coll.;* southwest corner of Cayuga Lake, *Jackson,* 1903; Cascadilla Glen. CATTARAUGUS CO.: Waterman Swamp, Napoli (Boehner 1943, p. 14). CORTLAND CO.: Robbins Glen, Truxton, *Wiegand,* 1893; West Hill woods, Truxton, *Wiegand,* 1892.

This species occurs under similar conditions as *F. eboracensis* locally, namely, on the bark of trees, predominantly deciduous trees.

The absence of a line of "ocelli" running through the dorsal leaf-lobes distinguishes it at once from *F. asagrayana* from which it can usually be separated by the somewhat inferior size. Superficially it is very difficult to distinguish from *F. eboracensis* but it differs at once (when fruiting) in having a more slender beak at the tip of the perianth and in having the upper part of the perianth tuberculate, especially on the keels. Under the microscope sterile materials may be separated from *eboracensis* because of the presence of distinct outer teeth (one on each side) of the bilobed amphigastria.

F. OAKESIANA Aust.

Very rare, local. CATTARAUGUS CO.: "on bark of trees in Waterman Swamp, Napoli" (Boehner 1943, p. 14, listed as *F. kunzei,* "Det. by L. Clark").

This rare species has not been previously recorded south of the Coniferous Zone of the White Mountains from which it was originally described. It occurs most often, northward at least, on the bark of *Thuya* and other conifers, often in swamps and at the margins of bogs. There have been no previous reports of it from near the Deciduous Zone. Associated species are most often *Lejeuna cavifolia, Radula complanata* and other species of *Frullania.* Like these last species, it is essentially a pioneer on the bark of living trees, apparently never invading bare rock walls.

It is the smallest and most delicate of our species of *Frullania.* It is therefore not likely to be mistaken for any of them but may be mistaken for the equally minute *F. selwyniana* (not yet found in this region). From all of our other species of the genus it differs at once in the very large galeate lobules which are usually 3/5 as large as the dorsal lobes (or may even approach them in size). In addition, the autoecious inflorescences (and nearly constant presence of them) are diagnostic. The androecia are very short and subglobose, never spike-like. The cell-walls are generally almost evenly

thickened, showing only minute trigones. In the field the more or less bright reddish or purplish-brown color is characteristic, as well as the minute size.

For some reason not quite clear to the writer this species was listed in Boehner (1943) as the entirely unrelated *F. kunzei* Lehm. & Lindenb., a species not even belonging in the same subgenus. Although the two species share an autoecious inflorescence, they differ very widely in the shape and size of the lobules as well as in numerous other features (see key). Through the courtesy of the Rev. P. Boehner I have been able to check the specimen.

F. INFLATA Gottsche

Rare. TOMPKINS CO.: On bark of tree at edge of Ringwood Swamp, *Schuster* 1943; record somewhat doubtful.

This species, like all of the above, is a xerophyte and is either corticolous or epipetric. It and all our other species of the genus, belong to the various lociules of the widely distributed primary *Frullania-Radula* Associule invading dry vertical rock surfaces or the bark of deciduous trees or of the conifer *Thuya*. Among the various species, *F. inflata* is among the least xeric in its adaptative features (the generally dark green color and explanate lobules are correlated with largely less extremely xeric occurrences) and is often decidedly calciphilous. It should be found in our area on calcareous shales and sandstones.

The collection cited above cannot be referred to any other species. Virtually all of the ventral lobes examined in the scanty material were explanate; the plant was entirely deep green. Since material of our common species, *eboracensis* is not infrequently green and since it occasionally has a few of the lobules explanate, it may possibly be found that the present collection is a mesic extreme of *eboracensis*. The explanate lobules of the present species are generally sufficient to distinguish it from all other species of the genus likely to occur in our region.

Suborder 2. METZGERINAE (Jungermanniales Anacrogynae)

KEY TO GENERA

1. Rhizoids purple; gametophyte divided into a stem and succubous, wavy or crispate, irregular, rectangular leaves (Pl. 18, fig. 1) ..... *Fossombronia*

1. Rhizoids colorless or pale brownish; gametophyte thalloid, at most with shallow lateral scalloping of the lamina (Pl. 15, figs. 1-8) 2

2. Margins of thallus with hairs (Pl. 18, fig. 3); costa very sharply defined, the lamina unistratose suddenly on each side; delicate yellow-green linear plants less than 2 mm wide, branching dichotomously; sex-organs on short ventral branches (Pl. 18, fig. 3); seta less than 2 mm long ..... *Metzgeria*

2. Margins of thallus lacking hairs (Pl. 15, figs. 1-9); costa present or absent, if present disappearing gradually into the lamina; sex-organs dorsal or lateral; seta elongate, over 5 mm long 3

3. Costa entirely absent; inflorescences on short lateral branches; calyptra large, clavate, not surrounded by a pseudoperianth (Pl. 15, figs. 1-3, 7) ..... *Riccardia*

3. Costa present, though not very sharply defined (Pl. 15, figs. 6, 9); sex-organs dorsal on thallus (Pl. 15, figs. 5, 8); calyptra small, surrounded at least at base by an involucre (pseudoperianth) (Pl. 15, fig. 5); large species 4

4. Dark, opaque spots present at the base of marginal, shallow lobes of the lamina (Pl. 15, fig. 4); ovate, dentate small ventral scales present; thallus strongly, somewhat dichotomously branched; gemmae always present (Pl. 15, fig. 4) ..... *Blasia*

4. Thallus lacking lateral lobes, lacking dark opaque auricles; ventral scales entirely absent; not or weakly branched; gemmae absent 5

5. Female involucre of an outer ring of fringed, laciniate scales, the inner a long, tubular pseudoperianth (not appearing until long after the outer ring) (Pl. 15, figs. 5, 8); sex-organs not sunk in pockets, the antheridia under toothed dorsal scales; costa very distinct, strongly convex beneath (Pl. 15, figs. 6, 9) 6

6. Costa with a central ligneous strand of opaque cells (visible by strong transmitted light without sectioning) (Pl. 15, fig. 9); thallus subsimple, narrowly linear, the lamina not wavy (Pl. 15, fig. 8); spores 20-24 μ ..... *Pallavicinia*

6. Costa without a central ligneous strand (Pl. 15, fig. 6); thallus rather freely branched, short-lingulate, the lamina crisped and undulate (Pl. 15, fig. 5); spores 30-50 μ ..... *Moerkia*

5. Female involucre of a single low ring, or a simple flap, never with an outer ring of scales; sex-organs sunk in dorsal pockets, the antheridia not under toothed scales along the costa; costa scarcely distinct, very gradually disappearing into the lamina ..... *Pellia*

Family FOSSOMBRONIACEAE

I. FOSSOMBRONIA Raddi

F. WONDRACZEKII (Corda) Dumort.

Frequent locally, but usually in small quantities. TOMPKINS CO.: Sixmile Creek Ravine, on loamy banks and near their crest on sterile moist soil, *R. M. & O. M. Schuster;* South Hill, middle of path, *Schuster;* Old Buttermilk Glen, *Schuster;* Brooktondale, *Ford;* Enfield Glen, *R. M. & O. M. Schuster;* 2-3 miles south of Dryden, *R. M. & O. M. Schuster;* Varna, *Schuster;* between Dryden and Ringwood, *Schuster.* TIOGA CO.: along canal bed near Richford, *Andrews;* loamy banks in hills east of Caroline, *Schuster.* CATTARAUGUS CO.: "with *Anthoceros laevis* L., and just about as common" (Boehner 1943, p. 14).

A species exclusively of denuded, exposed soil lacking organic matter, occurring on loamy and clayey or sandy-loamy moist soils, often on banks and in the middle of old wagon-roads in woods or in paths. A frequent accessory species of the *Anthoceros-Blasia* Associule of the Transition Zone, associated with *A. laevis, punctatus, crispulus,* rarely with *A. macounii* and almost invariably with *Blasia* on wet banks or with *Pellia* on moist banks. Relatively rarely *Notothylas* enters this associule while *Riccardia pinguis* enters it when the society is growing on banks. Under somewhat less mesohygrophytic conditions the *Fossombronia* enters into a society with *Plectocolea crenulata,* accompanied on relatively shaded banks by *Pellia epiphylla,* on more exposed, often acid, leached soils by *Lophozia bicrenata* and *Cephaloziella.* The main requirements of the species appear to be a moderately constant supply of moisture (hence it is limited to water-retaining soils of a very heavy consistency), absence of much organic matter and absence of much crowding; it does not appear to be able to compete with the larger thalloid species which may rapidly grow out and over it. The species appears to have a moderate tolerance for lime, occurring on banks with such vascular species

as *Eupatorium urticaefolium* and *Lobelia syphilitca*, mentioned as indicators of calcareous conditions by Wiegand and Eames. The absence locally of other species of *Fossombronia* may be due to lack of such a tolerance for lime. Capsules are produced abundantly and are observed usually between September 15 and October 15, with a maximum discharge of spores about September 25-October 5.

The purple rhizoids and the occurrence on clayey or loamy soil, are usually sufficient to identify this species. The occurrence of distinct leaves and axis (Pl. 18, fig. 1) separate it at once from other Metzgerinae. Confusion is more likely with Jungermanninae from which the dorsal position of the involucres will distinguish it; we further lack other pale green species possessing purple rhizoids. The usually crispate, wavy, irregular leaves with very large, thin-walled cells are also characteristic.

Family PELLIACEAE

I. BLASIA (Mich.) L.

B. PUSILLA L.

Frequent locally. TOMPKINS CO.: Enfield Glen, *sev. coll.*; Sixmile Creek Ravine, *Schuster;* Varna, *Schuster;* Coy Glen, *Ford & Schuster;* Old Buttermilk Glen, *R. M. & O. M. Schuster;* two miles south of Dryden, *R. M. & O. M. Schuster;* east of West Danby Station, *Eames.* TIOGA CO.: Richford, in large quantities along many banks of hill-side roads. MONROE CO.: Irondequoit Bay, *R. M. & O. M. Schuster.* CATTARAUGUS CO.: Birch Run Road, Allegany; Martiny Rocks; Vandalia (*Boehner* 1943, p. 14). ONTARIO CO.: Briggs Gully, Richmond, *Schuster.* ONONDAGA CO.: Hopper's Glen (Goodrich 1912, p. 22).

Found under similar conditions as *Fossombronia wondraczekii* but preferring somewhat moister or somewhat more shaded conditions; also occurring on thin soil over wet, dripping ravine-ledges on non-calcareous rocks with *Pellia epiphylla* or directly on the rock; more rarely occurring on wet, saturated, alluvial, sandy deposits in the bottom of the ravines as at Enfield Glen, associated with *Anthoceros laevis* and *Notothylas*. A dominant member of the *Anthoceros-Blasia* Associule of loamy, moist or wet banks or shaded, moist paths and wagon-roads; occurring also as a *Blasia* facies on very moist or wet banks, often with a coverage approaching 100% locally and from 50-90% over wide areas. Able to tolerate lime but apparently limited in distribution in calcareous regions.

The coarsely scalloped thallus margins and free dichotomous branching (often thus resulting in rosettes) as well as the possession of small but persistent ventral scales and dark spots (auricles) of the lamina at once separate this very distinct species. The almost invariable occurrence of gemmae is also characteristic (Pl. 15, fig. 4).

II. PELLIA Radii

KEY TO SPECIES

1. Monoecious; involucre flap-shaped, near thallus apex; antheridia present as raised or conical papillae behind female involucre; thallus in cross-section with thickened bands; elaters slender, to 500 μ ..... *P. epiphylla*

1. Dioecious; involucre a complete ring, not flap-shaped.
   2. Thallus with vertical thickened bands in longitudinal section; involucre a low collar, beyond which the calyptra is long-emergent; elaters as in *P. epiphylla* ..... *P. neesiana*
   2. Thallus without vertical thickening; involucre large, tall, the calyptra immersed; elaters thick, to 200 μ long ..... *P. fabbroniana*

P. EPIPHYLLA (L.) Corda

Frequent. TOMPKINS CO.: Sixmile Creek Ravine, *R. M. & O. M. Schuster;* Sixhundred Ravine, *sev. coll.;* Varna, *Schuster;* Enfield Glen; Malloryville; McLean Bogs, near edges of *Sphagnum* bog; 3 miles south of Dryden near headwaters of Sixmile Creek, *R. M. & O. M. Schuster.* CORTLAND CO.: west of Solon along creek-bed, *Schuster & Winne.* TIOGA CO.: Loamy banks along roadsides in Richmond, *R. M. & O. M. Schuster.* CHENANGO CO.: Plymouth Pond, with *Scapania paludicola* and *irrigua, Schuster & Winne.* MONROE CO.: Irondequoit Bay, *R. M. & O. M. Schuster.* SENECA CO.: Swampy, acid woods near Junius Bogs, *Schuster.* ONONDAGA CO.: Tamerac Swamp (Goodrich 1912, p. 23). ONTARIO CO.: Briggs Gully, Richmond, *Schuster.* ERIE CO.: Smoke's Creek, W. Seneca (Day 1882, p. 165). CATTARAUGUS CO.: St. Bonaventure; Connoisarauly Creek; Chamberlain's Bog, Steamburg; Cold Spring; Beehunter Creek, Allegany State Park (Boehner, 1943, p. 14).

Not a really abundant species throughout much of our area, perhaps because it does not appear to tolerate more than small amounts of lime. Occasionally it occurs on thin soil over wet shale or sandstone or on the rock itself but then only on non-calcareous rocks. In our area much more common on moist, loamy or sandy-loamy roadside banks, along streams and ditches and on loamy soil, entering into the *Anthoceros-Blasia* Associule usually as an important accessory species, rarely as a dominant species. Generally occurring under conditions of either greater exposure or lesser moisture or both, as compared with *Blasia;* frequently strongly reddish-pigmented when in direct light, which rarely occurs in *Blasia.* Occasionally (as at Plymouth Bog and at the edges of Plymouth Reservoir) occurring growing on decaying logs with species like *Riccardia palmata* and *latifrons* and *Blepharostoma* and *Lepidozia reptans.* Fruiting freely in our region from April 15-May 5, usually.

This and the following two species are superficially very similar; they can be differentiated from other genera by the weakly differentiated costa (absent in *Riccardia,* more distinct in our other genera), the large size, subsimple condition, and often leathery texture (less so in *P. fabbroniana*) and the reduced, simple involucral rings.

The more leathery texture, the usual occurrence (either on old, decaying parts of the plant, or on young, living parts) of the characteristic flap-like or scale-like involucres, the often largely reddish-pigmented thalli, and the lack of toleration of lime, separate this species from the usually more hygrophytic *P. fabbroniana.*

P. FABBRONIANA Raddi

Infrequent, local. TOMPKINS CO.: Fall Creek Ravine, *Schuster* 1942; Enfield Glen, *sev. coll.* MADISON CO.: Chittenango Falls (material doubtful), *R. M. & O. M. Schuster.* ONONDAGA CO.: "Harbor Ditch" (Goodrich 1912, p. 23, as *P. endivaefolia*). CATTARAUGUS CO.: Martiny Rocks, West Branch of Four Mile Road; Allegany; Mt. Moriah, Vandalia; Conewango Swamp; Stoddard Creek, Allegany State Park; Rock City; Olean; Waterman Swamp, Napoli (Boehner 1943, p. 14).

A decidedly calciphilous species, always occurring under almost or quite hygrophytic conditions in our region, usually on shaded to semi-exposed, dripping or wet vertical ravine-walls, on moist ledges or cliffs or on the talus at their feet, occasionally on moist clayey soil and calcareous banks. Commonly associated are *Preissia quadrata, Riccardia pinguis, Conocephalum conicum* and *Lophozia badensis*. At times forming a distinct union with the *Preissia*, at other times occurring under slightly more mesophytic, shaded conditions with the *Lophozia*. The numerous records given by Boehner (1943) for Cattaraugus County and the non-calcareous habitats from which he records the species, make one wonder if the records do not possibly refer to *P. epiphylla* in part.

The erect, tubular involucres found usually on the older portions of plants, and the more delicate structure, differentiate this species from *P. epiphylla*.

P. NEESIANA (Gottsche) Limpr.

Apparently quite rare and local. CATTARAUGUS CO.: "on moist soil along the South Branch of Cattaraugus Creek, Gowanda" (Boehner 1943, p. 14); determination verified by writer.

This species is unreported from elsewhere in our region but is to be expected. The species in many regions is more common at higher elevations than *P. epiphylla* and is therefore not to be expected throughout much of our area. The favorite habitat is along the edges of streams and brooks, in wet ditches and similar places. Though not a "calciphile," the species seems more tolerant than *P. epiphylla*.

The generally determinable dioecious inflorescence together with the presence of vertical thickened bands of the thallus, separate this species from both our other species. The non-calcareous habitats this species usually prefers automatically eliminate *P. fabbroniana* from consideration. Female plants are separable easily by the form of the inflorescence: the involucre is essentially flap-shaped as in *epiphylla*, and is nearly or quite horizontal; however, the involucre forms a complete ring with the anterior portion of the ring so much lower than the posterior that it may appear absent (in *epiphylla* the involucre is more flap-shaped and does not form a complete ring). In both this species and *epiphylla* the involucre is relatively low and is much exceeded by the calyptra as the sporophyte approaches maturity.

Family PALLAVICINIACEAE

1. MOERKIA Gottsche

KEY TO SPECIES

1. Thallus extremely strongly crispate, robust, the female plants from 4.5 to 7 mm wide; costa obtrapezoidal, in section 16-25 cells high; the spores mostly 40-50 μ ..... *M. flotowiana*

1. Thallus more delicate, slightly to moderately undulate-wavy, the female plants from 3-4.2 (4.5) mm wide; costa more or less triangular in section (the keel ventrally forming an obtuse angle: not with a flat ventral surface), in section 14-16 (or less) cells high; spores 30-38 μ ..... *M. hibernica*

M. HIBERNICA (Hook.) Gottsche

Rare and local. TOMPKINS CO.: Sixmile Creek, March 26, 1944, *R. M. & O. M. Schuster,* with mature sporangia. GENESEE CO.: along marly ditch on south edge of Bergen Swamp, 1945, *R. M. & O. M. Schuster;* on edges of open part of marl bog, Bergen Swamp, *Schuster & Winne.*

This species and the next are locally virtually impossible to keep apart and all our material should perhaps be cited under one species. Both forms locally (in so far as they are distinct) behave rather similarly ecologically. Both are calciphytes, occurring in areas where there are small to large quantities of free lime available, and essentially on humus-poor substrates (see *M. flotowiana*). In spite of the fact that Meylan (1924) emphasizes the "calcifuge" nature of both this and the next species, they are typical calciphytes in northeastern America, occurring restricted largely to marl bogs (accompanied always by *Thuya*), or in ravines, associated with marly, springy areas or somewhat calcareous outcrops of sedimentary rocks. Müller (1905-1916, p. 360) has stressed the fact that *hibernica* occurs on lime-rich ground.

All the local material of *Moerkia* for some time was called *M. flotowiana* for the following reasons: the thallus-wings in local material are in almost all cases strongly undulate (supposedly "non ou faiblement ondule au bord" in *hibernica*) and the plants when well developed are 3.6 to 4.2 mm wide or more (*fide* Müller 1905-1916, those of *hibernica* are 2-3 mm wide, those of *flotowiana* 4 mm wide; Meylan 1924, p. 108, however, gives those of *hibernica* as "ayant au plus 4 mm de largeur," while those of *flotowiana* attain 4-5 mm in width). The entire general appearance of all the local material therefore suggests *flotowiana.* However, the cross-sections of the thallus of the material placed here in *hibernica* show a more or less triangular costa, mostly 14-16 cells high (in *flotowiana* trapezoidal and supposedly 16-22 cells high). Of even more importance, the material from Sixmile Creek was collected with ripe capsules and the spores measure only 30-38 μ, mostly (12 spores measured; 3 measured 30 μ; 5, 34 μ, 3, 38 μ, and 1, 41 μ). This agrees more closely with the range of 30-34 μ given by Meylan for *hibernica* than the 40-50 μ given for *flotowiana.*

It is apparent therefore that the differences cited in the manuals between these two species are not as sharp as they would appear. It is further apparent that much of the material which has been called *flotowiana* by American workers will probably turn out to be *hibernica,* on more critical study. Dr. K. Müller, to whom I submitted material of *Moerkia* from both the Sixmile Creek locality and northeastern Minnesota, has called both *hibernica. M. hibernica* has been previously reported only once from the United States (Washington, D. C.) and a single time from Ontario (Huntington, North Hastings); elsewhere in North America it has been found only in the far west (Canadian Rockies, British Columbia, Alaska).

M. FLOTOWIANA (Nees) Schiffn.

Rare and local, apparently widely distributed. TOMPKINS CO.: Sixmile Creek Ravine, below Potters Falls, *R. M. & O. M. Schuster.* ONTARIO CO.: Briggs Gully, Richmond, *Schuster.* Previously unreported for New York.

This very local species appears to be rather widely distributed under cal-

careous or subcalcareous conditions. It occurs chiefly on marly, wet, springy slopes and banks, on thin soil over wet, calcareous shale or growing directly on the shale itself, or on the wet edges of ditches. Almost always associated are *Conocephalum* and *Trichocolea;* frequently associated is the scouring-rush, *Equisetum variegatum,* among the clumps of which *Moerkia* often occurs as isolated plants. *Riccardia pinguis* is constantly found associated with it and occasionally either *R. multifida* or *R. sinuata. Preissia* also frequently is an accessory species. A decidedly hygrophytic species, able to tolerate moderately direct light but most common in shade (often occurring on the protected, shaded side of shale talus-fragments); apparently definitely influenced in its distribution by the presence of at least a minute amount of lime.

The record of the similar-appearing *Pallavacinia lyelli* from Onondaga County, by Goodrich, possibly belongs here since the latter species is absent in the ravines, is a decided "calciphobe," and is limited to bogs and swamps in our area; *Moerkia* on the other hand, occurs in either ravines or on marly soil.

The habitat as well as the large size, rather transparent thallus wings that are characteristically undulate and crispate (Pl. 15, fig. 5), as well as the frequently occurring dichotomizations or lateral branches, distinguish this species. The most characteristic features of the thallus is the crisped, wavy aappearance which alone will separate it from both the closely allied *Pallavicinia* as well as all other thallose forms. The double involucre is usually present on at least some plants; the outer consists of laviniate scales that are not connate basally to form a distinct collar (*Pallavacinia* however, has them more or less fused basally into a distinct collar). In cases of doubt, the absence of a central strand of thickened, ligneous cells running through the costa separates it from *Pallavicinia;* this strand can easily be seen in the latter by examination of the fresh or soaked thallus by bright transmitted light.

The material from Briggs Gully had the thallus sections with the costa obtrapezoidal and 16 to 20 cells high; furthermore the plants were greatly crispate and the female ones 5-7, occasionally even 8 mm wide. These plants were considerably more robust than the material from Tompkins County and Bergen Swamp, and are on the basis of gametophytic characters, to be referred to *M. flotowiana.* The costa showed no trace of the fine lateral strands of small cells but much of the material of *flotowiana* lacks such strands and therefore no distinction between it and *M. hibernica* is possible on the basis of this characteristic.

The collection from Sixmile Creek (April 27, 1946) is also, in my estimate, typical *flotowiana.* It has the thallus strongly crispate, 5-7 mm wide on female plants, with the costa obtrapezoidal in cross-section, 16-20 cells high and showing a vestigial "strand" on each side (consisting of several more hyaline cells in younger parts of the thallus; of more brownish cells in older parts of the thallus); the spores were 38-45 μ.

In contrast, the collection from Sixmile Creek (March 26, 1944; referred to *hibernica*) in which the spores measured 30-38 μ, differed slightly in vegetative characters from the above. The thallus was somewhat less crispate,

the maximum width of female plants was 4-4.5 mm and the costa was more nearly broadly triangular in cross-section with the height on a female plant about 14-16 cells. This collection then, in the sum total of its characters is closer to *hibernica*. No trace of the pair of strands could be demonstrated in the costa of this collection.

II. PALLAVICINIA Gray, corr. Carr.

P. LYELLI (Hook.) Gray

Rare, locally abundant. TOMPKINS CO.: Woodwardia Bog, *R. M. & O. M. Schuster;* upper course of Newfield Brook, *Andrews*, det. by Andrews; McLean Bogs, *Schuster*. SENECA CO.: Junius Peat Bogs, *R. E. & E. Schuster*. ONONDAGA CO.: Howlett Gorge (Goodrich 1912, p. 23). CHENANGO CO.: Plymouth Pond, near Plymouth, among *Sphagnum* of moor, *Wiegand, 1916;* sphagnous outlet of Plymouth Sphagnum Bog, *Schuster & Winne, 1946*. CATTARAUGUS CO.: Steamburg. (Knobloch 1934, p. 10;) "found in all our swamps and bogs" (Boehner 1943, p. 14). CAYUGA CO.: Featherbed Bog, *Erica Gaertner*.

In most of central and western New York this predominately coastal plain species is quite rare, largely because of an apparent inability to tolerate any lime in its substratum. It is therefore almost invariably confined, in our area, to areas near bodies of standing water on mucky soil very rich in organic matter at the edges of swamps, on decaying wood in such regions or among Sphagnum of bogs (Plymouth Pond and Junius). The only exception to this rule is the occurrence of this species along a sphagnous brook leading from Plymouth Bog where the species is abundant under semi-aquatic conditions. Almost invariably associated are *Cephalozia connivens* or *Cephalozia media*, occasionally *Cladopodiella*, *Mylia* and other members of the *Mylia* Associule, *Calypogeia sphagnicola* and *Lophozia marchica*. Apparently absent in the ravines or in ditches where running water could possibly saturate the substratum with lime; in acidic regions not infrequent on moist humus along brooks and rivulets.

The elongate lingulate, usually simple thallus with a distinctly defined costa, and with the somewhat hyaline lamina not or scarcely undulate (Pl. 15, fig. 8), differentiate this species. It differs from the strongly crispate *Moerkia flotowiana* further in possessing a distinct central ligneous strand (Pl. 15, fig. 9) of the costa (demonstrable on holding the thallus up to a bright electric bulb), in the much smaller spores (less than 25 μ rather than over 40 μ) and in the complete ring formed by the laciniate scales of the outer involucre.

Family METZGERIACEAE

I. METZGERIA Raddi

KEY TO SPECIES

1. Wings with hairs mostly paired, arising strictly from the margins (Pl. 18, fig. 3); hairs absent or nearly on lower side of thallus-lamina; cells mostly 45-60 μ; monoecious; gemmae never present; mid-rib always developed ..... *M. conjugata*

1. Wings with hairs always single, often nearly absent, arising from just within margin, and directed downward, i.e., submarginal; often with hairs on lamina ventrally; cells mostly 32-42 μ, often somewhat smaller; dioecious; gemmae often present, oval to elliptical; often lacking midrib ..... *M. furcata*

M. FURCATA (L.) Dumort.

Exceedingly rare locally. TOMPKINS CO.: Lick Brook Ravine, 5 miles south of Ithaca, March 16, 1946, *R. M. Schuster, Walter Scudder.* TIOGA CO.: Headwaters Swamp, *W. C. Muenscher & B. Brown.*

I place here with a little hesitation, a very curious, juvenile *Metzgeria.* The plant involved grew 4-6 feet above ground on the bark of yellow birch *(Betula lutea)* associated with a somewhat depauperate form of *Ptilidium pulcherrimum* and a leptodermous form of *Frullania eboracensis;* lower down near the roots, occurred some *Lejeunea cavifolia* and *Porella platyphylloidea.*

This form totally lacks any indication of a mid-rib in even the oldest plants present; the size is minute compared with *M. conjugata.* It agrees tolerably well in all regards with the var. (?modification) *ulvula* Nees of *M. furcata*: the pale yellowish green color of its cushions, the very rarely furcate thallus, especially the presence of numerous oval to elliptical, sublinear marginal gemmae standing out at right angles to the parent plant, all agree perfectly with the *ulvula* of Nees. Furthermore, the variety *ulvula* lacks a midrib or at best, a weak indication of one in the gemmae and therefore is also to some degree a persistent juvenile form.

Since *M. conjugata* occurs abundantly in Lick Brook Ravine, both on moist shaded rocks and on bark of Yellow Birch at 1-2 feet above ground, it was felt that the present form may be a juvenile form of that species. The scarce marginal hairs of the thallus, occurring always singly and always present just within the margin, i.e., arising from the ventral side of marginal cells rather than from the outer side, all indicate that the present form belongs in *M. furcata* rather than in *conjugata.* Furthermore, gemmae in *M. conjugata* are according to various authorities, "never present" (Macvicar) or rare. Finally, I have never seen *M. conjugata* occurring so far above ground on bark anywhere in the northeastern United States; the few records from bark are always from near the tree bases — and such forms in Lick Brook, totally lack gemmae, have distinct mid-ribs and marginal, geminate hairs and are entirely different in facies from the present form.

In view of these facts I feel that the present form should be placed under *M. furcata.* The frequent occurrence of *M. conjugata* locally and the nearly total absence of *M. furcata,* are a little mystifying but are perhaps due to the ability of the former to grow luxuriously under calcareous and subcalcareous conditions while *M. furcata* appears able to tolerate only extremely minute amounts of lime.[29]

The report of the Tioga County material reached me after the above was written; the material here also occurred on the bark of *Betula lutea.*

The more xerophytic nature of the present species, its occurrence on relatively exposed, drier rocks or far up on the trunks of trees, separate it

29 Systematic search more recently, has resulted in the discovery at Lick Brook, of a second colony, on the bark of *Ulmus fulva,* associated with *Microlejeunea ulicina* and *Frullania eboracensis.* The material here is more typical and many of the older thalli clearly showed the mid-rib to consist of two rows of cells dorsally and ventrally, as in the variety *ulvula.*

from the more strictly mesophytic or mesohygrophytic *M. conjugata* which differs also in commonly having the marginal cells provided with paired, strictly marginal hairs (submarginal and always single in *M. furcata*).

M. CONJUGATA Lindb.

Locally common. TOMPKINS CO.: Sixmile Creek Ravine, *Schuster, 1942;* Sixhundred Ravine, *Andrews & Schuster;* Coy Glen, *sev. coll.;* Enfield Glen, *sev. coll.;* Old Buttermilk Ravine, *R. M. & O. M. Schuster;* Lick Brook, *Schuster; Buttermilk Glen, sev. coll.;* Renwick Brook, *R. M. & O. M. Schuster;* McKinney's Twin Glens, *R. M. & O. M. Schuster;* Taughannock Ravine, *Schuster & Matthysse;* Fall Creek (formerly, now extinct), *Wiegand;* Cascadilla (formerly, now extinct), *Wiegand.* SCHUYLER CO.: Watkins Glen, *Schuster.* MADISON CO.: Chittenango Falls, *R. M. & O. M. Schuster.* ONONDAGA CO.: Cazenovia Road (Goodrich 1912, p. 23); Syracuse, on birch bark (Underwood & Cook, Hep. Amer., No. 46). CATTARAUGUS CO.: Martiny Rocks, Allegany; Stoddard Creek, Allegany State Park (Boehner 1943, p. 14).

Apparently a "calciphilous" species, limited strictly to the ravines or to subcalcareous and calcareous shale and sandstone outcrops. In other regions occurring occasionally entirely away from all calcareous substrata but in our region not known in the ravines that cut through only non-calcareous rocks (Briggs Gully). Usually associated with such calciphilous species as *Reboulia hemisphaerica* as well as the calciphilous ferns *Cryptogramma stelleri, Pellaea atropurpurea* and *Camptosaurus rhizophyllus.* Very rarely in our region, invading the exposed, moist, shaded roots of trees near rock-outcrops as at Sixmile Creek and Buttermilk Glen, never occurring more than two feet above the bases of trees, as at Lick Brook. Occurs most luxuriously on densely shaded outcrops and is apparently limited to the Hemlock Ravine Community. The species occurs under decidedly more shaded conditions than the *Preissia-Conocephalum-Riccardia pinguis* Associule of exposed, wet-to-dripping cliffs and talus, and usually is decidedly less hygrophytic. Generally occurring with *Metzgeria* are species of *Radula,* exceptionally *R. complanata* (under semi-xerophytic, exposed extremes of occurrence), more often *R. obconica* and *R. tenax;* frequently *Lejeunea cavifolia,* occasionally *Cololejeunea* enter into association with it. Our most tolerant species as regards very diffuse light, often occurring on the under side of moist horizontal shale outcrops and ledges where direct sunlight never hits; there occasionally accompanied by *Lejeunea.*

The small size and the very elongate, narrowly-lingulate, pale to yellow-green thallus, branching apparently dichotomously, with a sharply defined costa separated from the unistratose lamina, as well as the unique marginal hairs commonly occurring in pairs, separate this species from all other Hepaticae except the above species.

Family RICCARDIACEAE

I. RICCARDIA Gray, emend. Carr.

KEY TO SPECIES

1. Very large, subsimple species (Pl. 15, fig. 1), thick, opaque; thallus medially 10-15 cells thick, bright green and greasy in appearance; thallus mostly 4-8 mm wide; dioecious ..... *R. pinguis*

1. Smaller species, the thallus to 2 mm wide, more or less strongly branched (Pl. 15,

figs. 2-3, 7), the branches translucent, usually deep or bluish-green; thallus 9 or less cells thick in the middle.

2. Thallus regularly 3-pinnately branched (Pl. 15, fig. 2) the ultimate branches with a hyaline unistratose border 2-3 cells wide ..... *R. multifida*

2. Thallus bipinnately or irregularly, sometimes somewhat palmately branched, never regularly tripinnate (Pl. 15, figs. 3, 7); ultimate branches with the unistratose, hyaline border 1 cell wide or absent.

3. Thallus more or less pinnately branched, thin, dark-green; section 6-9 cells thick in middle; on moist rocks ..... *R. sinuata*

3. Thallus irregularly branched or somewhat palmately branched; always on rotting wood or organic substratum.

4. Branching irregular, the ultimate branches short lingulate, usually broadened apically (Pl. 15, fig. 3); cross-section 5-6 cells thick in middle, plano-convex; monoecious ..... *R. latifrons*

4. Branching usually subpalmate, the ultimate branches mostly linear, narrowed apically (Pl. 15, fig. 7); cross-section 6-9 cells thick in the middle, biconvex; dioecious ..... *R. palmata*

R. SINUATA (Dicks.) Trev.

Very rare locally. ONTARIO CO.: Briggs Gully, Richmond, near south end of Honeoye Lake, Oct. 1945, *Schuster*. TOMPKINS CO.: Enfield Glen, 1944, *R. M. & O. M. Schuster*. CATTARAUGUS CO.: "on a wet stone growing among mosses along . . . South Branch of Cattaraugus Creek, Gowanda" (Boehner 1943, p. 15)

This is one of our rarest species of hepatics; both of the writer's collections consisted of only a little material. The Ontario County material is quite typical but there is a little doubt about the material from Tompkins County; no other disposition of it seems possible however, since the marginal unistratose border present in *R. multifida* is absent.

Occurring almost always on wet, usually dripping rocks; never on rotting logs or on humus. Apparently with at least a slight toleration for lime since it was accompanied at both stations by calciphilous Hepaticae and occurred on subcalcareous shale. At Briggs Gully, growing associated with *Moerkia flotowiana, Riccardia pinguis* and *Conocephalum;* at Enfield Glen, growing among *Thuyidium* over wet rocks with *R. pinguis, Preissia* and *Conocephalum*.

The 1-2 pinnate branching and the absence of any indication of a unistratose hyaline border of the thallus, adequately differentiates this species usually. The habitat at once differentiates the species from the irregularly branched *R. latifrons* and the palmately branched *R. palmata*. The similarly branched *R. multifida* may also occur on wet rocks; it differs at once in the usually more copious branching, the presence of an unistratose border 2-3 cells wide and the usually narrowed tips of the branches.

R. MULTIFIDA (L.) Gray

Very rare, local. GENESEE CO.: Edge of Bergen Swamp, along a calcareous, wet ditch along railroad tracks, April 1945, *R. M. & O. M. Schuster; Thuya* swamp at Bergen, at edge of open marl, with *R. pinguis, Moerkia,* and *Lophozia rutheana,* etc., 1946, *Schuster & Winne*. CATTARAUGUS CO.: "on very wet stones along Beehunter Creek, Allegany Park" (Boehner 1943, p. 14).

The writer's records of the species are from a distinctly calcareous region.

The species occurred on the steep side of a ditch of gravel and cinders, associated with *Preissia, Moerkia flotowiana,* and *Equisetum variegatum;* fruiting April 28, 1945.

This species differs from all our other forms in having the apical branches with a distinct wide, hyaline border only a single cell thick, appearing as a thin margin on the thicker, central portion of the thallus. It is most nearly related to *R. sinuata* under which the differences between the two are treated.

R. LATIFRONS (Lindb.) Lindb.

Frequent locally. TOMPKINS CO.: Enfield Glen, *sev. coll.;* Sixmile Creek Ravine, *Schuster;* swampy hillside 2-3 miles south of Dryden, *R. M. & O. M. Schuster;* Woodwardia Bog, *R. M. & O. M. Schuster;* Ringwood Swamp, *R. M. & O. M. Schuster;* Malloryville Bog, *Schuster & Rader;* McLean Bogs, *Schuster;* Headwaters Swamp, *Schuster;* Michigan Hollow Swamp, *Schuster;* Mud Creek, near Freeville; Dryden Lake, *Schuster.* CHENANGO CO.: On rotting log, along outlet of Plymouth *Sphagnum* Bog, *Schuster & Rader.* CAYUGA CO.: Paine's Creek near Aurora, *Schuster & Andrews.* CORTLAND CO.: Beaver Brook near South Cortland, *sev. coll.* GENESEE CO.: Bergen Swamp, *R. M. & O. M. Schuster.* ONTARIO CO.: Briggs Gully and vic., Richmond, *Schuster.* ONONDAGA CO.: Jamesville Road (Goodrich 1912, p. 21); White Lake, Dewitt, *Wiegand.* TIOGA CO.: Headwaters Swamp, *Schuster.* CATTARAUGUS CO.: South Branch of Cattaraugus Creek, Gowanda (Boehner 1943, p. 14).

Occurring in our area strictly on shaded, very moist or wet, decaying, decorticated logs, usually occurring in wet, densely shaded swamps or in the bottoms of shaded ravines. A characteristic member of the *Odontoschisma-Jamesoniella* Associule, accompanied by *Odontoschisma, Cephalozia media* and *catenulata, Cephaloziella rubella, Lophozia porphyroleuca* and *helleriana.* Generally occurring on or near the vertical sides of logs, with the *Cephalozia* while the other species are limited more to the less densely shaded dorsal sides.

The habitat alone is enough to differentiate it from all our other species except *R. pinguis* and *R. palmata* which may also occur on rotting logs. It differs from our other species in the rather copious but very irregular branching (Pl. 15, fig. 3), the older parts of the plant being so firmly attached to the substratum that removal is difficult, while the younger branches are usually suberect or ascending. When fertile, the monoecious inflorescence will aid in distinguishing it. Perhaps most easily confused with it is the much smaller, more regularly palmate *R. palmata.* This also occurs on rotting logs. It differs from *R. latifrons* in that the cortical cells of the thallus average only 50 x 30 μ or less (in latifrons 60 x 40 μ or more) and are much more strongly thick-walled than in the very thin-walled *R. latifrons.* Furthermore, gemmae occur abundantly while they are rare in *R. latifrons.* Other differences are indicated in the key to species.

R. PINGUIS (L.) Gray

Common but local. TOMPKINS CO.: Old Buttermilk Glen, *R. M. & O. M. Schuster;* Enfield Glen, *sev. coll.;* Coy Glen, *sev. coll.;* Sixmile Creek Ravine, *Schuster;* Headwaters Swamp, *R. M. & O. M. Schuster;* Fall Creek Ravine, *Schuster;* Varna, *Schuster;* headwaters of Sixmile Creek near Dryden, *R. M. & O. M. Schuster;* Forest Home, *Schuster;* McLean Bogs, *Schuster;* Freeville, fruiting Apr. 13, *Whetzel;* marly meadow south of

Dryden, *R. M. & O. M. Schuster;* Dryden Lake, *Schuster.* ONONDAGA CO.: Clark Reservation near Jamesville, *Rader & Schuster.* CORTLAND CO.: Morris Dam Truxtoo, *Wiegand.* GENESEE CO.: Bergen Swamp. ONTARIO CO.: Briggs Gully, Richmond. CAYUGA CO.: Paine's Creek near Aurora, *Andrews & Schuster.* CATTARAUGUS CO.: Lime Lake (Boehner 1943, p. 15).

A widely distributed species, occurring from under exceedingly marly conditions to decidedly acid conditions, as on rotting wood. Its local abundance may be traced to a great tolerance, if not a decided preference, for calcareous conditions. At Jamesville for instance, it grew on white, marly soil with *Preissia, Conocephalum* and *Asterella tenella* as well as on shaded, wet decaying logs. The species appears to thrive especially well on decaying logs lying over marly ground where both lime and organic matter are available for the plant. It is a common species on wet or moist ledges on ravine-walls, growing usually as small patches or individual plants, straggling among mosses, or growing on the talus at the foot of such ravines and cliffs; it is here usually associated with *Preissia, Conocephalum, Lophozia badensis, Pellia fabbroniana* and calciphilous mosses such as *Gymnostomum.* Also common on wet, marly, springy banks, or marly ditches, here associated very frequently with *Moerkia, Preissia* and *Riccardia multifida* but especially correlated in distribution with the northern scouring-rush, *Equisetum variegatum.* Under non-calcareous conditions it occasionally occurs together with *Pellia epiphylla, Blasia, Fossombronia wondraczekii* and *Anthoceros laevis* and *crispulus.* The chief requirement of the species is constant, abundant moisture and not too direct light. Under conditions of decided shade, it is usually dark green while in bright sunlight the appearance is usually bright or yellow-green.

The large size, turgid, greasy, opaque appearance, the characteristic color and the distinct odor when dry (and blackish-green color in that condition) are characteristic. The subsimple, broad, rather irregularly, very sparingly branched thalli (Pl. 15, fig. 1), differ very decidedly from the strongly branched thalli of all our other species. Confusion is most likely with other large thallose forms, especially *Moerkia;* it differs from the latter and all other thallose forms except the very different *Anthocerotales,* in entirely lacking a costa and in the thicker, opaque thallus, more brittle than in our other forms, and in lacking any unistratose lateral wings.

R. PALMATA (Hedw.) Carruth.

Rather rare, local. CHENANGO CO.: On decayed logs and stumps in swampy woods near edge of Plymouth Bog, *Schuster & Rader.* CATTARAUGUS CO.: "on a very wet bank in Conewango Swamp Leon" (Boehner 1943, p. 15). ERIE CO.: Buffalo and vicinity (Day 1882, p. 165); record seriously open to question since the species was much confused during the period before 1900.

This species occurs under identical conditions as *R. latifrons* and may occur intimately associated with it (as at Plymouth Bog). Other commonly associated species are *Blepharostoma trichophyllum, Lepidozia reptans, Cephalozia media, Jamesoniella* and *Jungermannia lanceolata* as well as *Nowellia* and *Odontoschisma.* Occurrences other than as a meso- or meso-hygrophytic xylicole are very exceptional.

This is our smallest species of *Riccardia* and it usually presents a very distinctive appearance. The more or less regularly palmate, or stag-like branching and the narrow, linear, often largely parallel-directed branches often tapering slightly towards their apices, are highly characteristic (Pl. 15, fig. 7). Under the microscope the thick, often reddish-tinged or brownish walls of the cells are distinctive and separate the species from all other *Riccardias*. When fertile, the dioecious inflorescence and prominent, linear androecia are highly diagnostic.

Marchantiales

KEY TO GENERA

1. Plants not in rosettes, the branching usually diffuse (Pl. 16, fig. 4; Pl. 17, fig. 6); ventral scales large, conspicuous, appendiculate (Pl. 16, fig. 3; Pl. 17, fig. 2); dorsal surface not sharply costate longitudinally, in middle; air-chambers opening by modified pores (Pl. 16, figs. 1-2, 5, 7). Sporophytes consisting of a foot, short seta, and brown capsule, borne in groups on stalked archegoniophoers (Pl. 16, fig. 4; Pl. 17, fig. 6) 2

2. Gemmae present; ventral scales with reniform appendages, hyaline, never purplish; ♀ receptacle divided into slender terete rays to near base 3

3. Gemmae receptacles crescentic; always sterile; surface of thallus shining, with inconspicuous areolation; only in greenhouses ..... *Lunularia*

3. Gemmae receptacles circular, cup-shaped; surface of thallus rather dull, with distinct impressed areolation; widespread ..... *Marchantia*

2. Gemmae absent; ♀ receptacle unlobed, or sharply lobed into flattened lobes (Pl. 16, fig. 4; Pl. 17, fig. 6) 4

4. Thallus extremely large (Pl. 16, fig. 4), 1.2-2.5 cm wide, 5-25 cm long, with very coarse, impressed areolation dorsally (conspicuous to naked eye); ventral scales hyaline, with rounded, semi-circular, basally constricted appendages (Pl. 16, fig. 3); plants never reddish; ♀ receptacle conical, high (Pl. 16, fig. 4) ..... *Conocephalum*

4. Thallus small or moderate in size, less than 8 mm wide and 3 cm long, with slight and inconspicuous areolation (Pl. 17, fig. 6); ventral scales usually purplish (as are the older thallus margins), with narrow, tapering appendages that are broadened basally (Pl. 17, fig. 2); ♀ receptacle disk-like or hemispherical or lobed 5

5. Moderate sized species, over 5 mm wide and usually over 2 cm long; pseudoperianth absent; dorsal epidermis firm, never becoming lacunose; female receptacles much less high than hemispheric 6

6. Pores simple (Pl. 17, fig. 1), scarcely visible to naked eye, little elevated, surrounded by 3-5 circles of cells; dorsal epidermis with distinct (often slightly bulging) trigones (Pl. 17, fig. 1); ♂ disks sessile a little behind the ♀ ones (Pl. 17, fig. 6); ♀ receptacle deeply 3-6-lobed (Pl. 17, fig. 6) ..... *Reboulia*

6. Pores compound, of several superimposed circles of cells (visible by focusing with the microscope), surrounded by only 2-3 circles of cells dorsally (Pl. 16, figs. 1-2); dorsal epidermis thin-walled, lacking trigones; ♂ disks stalked, appearing in summer; ♀ receptacles circular in outline, not lobed, appearing in spring ..... *Preissia*

5. Small species, less than 3 mm wide (except near apex of fertile plants). usually less than 2 cm long; pseudoperianth present, or dorsal epidermis becoming fissured, lacunose; female receptacle high, hemispherical, um-

bonate, or low-conical, scarcely lobed; pores simple, surrounded by only 1-2 circles of cells that are not thick-walled; epidermis thin-walled, lacking trigones; ♂ receptacles sessile on thallus 7

7. Pseudoperianth absent; dorsal epidermis delicate, by time of maturation of archegoniophores becoming fissured, spongiose-lacunose; usually green except for ventral scales ..... *Mannia*

7. Pseudoperianth present as a circle of narrow scales fringing the capsules; dorsal epidermis firm, persistent, never fissured ..... *Asterella*

1. Plants in rosettes, the branching close (Pl. 17, fig. 3); ventral scales (except in aquatic forms) minute or absent, not appendiculate; dorsal surface usually longitudinally grooved; air-chambers not surmounted by well-developed pores. Sporophytes reduced to a spherical capsule immersed in thallus (Pl. 17, fig. 3) 8

8. Epidermis lacking distinct pores, but often becoming spongy and lacunose with age (Pl. 17, fig. 3); ventral scales minute, virtually obsolete, never serrate; thallus-segments normally less than 4 mm wide; if aquatic, linear-dichotomous ..... *Riccia*

8. Epidermis with distinct pores, always firm; ventral scales (except in rare terrestrial forms) long, sword-like, purple, serrate; thallus-segments 5-9 mm wide; usually aquatic ..... *Ricciocarpus*

KEY TO STERILE MATERIAL (EXCEPT RICCIACEAE)

1. Ventral scales with large, reniform appendages that are constricted at juncture with scales (Pl. 16, fig. 3); large species 8-20 mm wide and 3-25 cm long; plants not at all purplish on edges or ventrally 2

2. Pores simple (Pl. 16, fig. 5); ventral scales in 2 rows; no circular gemmae cups 3

3. No gemmae cups; plants coarsely areolate (Pl. 16, fig. 4), dull, yellowish to brownish green ..... *Conocephalum*

3. With cresecntic gemmae cups: plant obscurely areolate, shining, pure green ..... *Lunularia*

2. Pores compound, with a cruciate opening (Pl. 16, figs. 1-2); ventral scales in 4-6 rows; with circular gemmae cups ..... *Marchantia*

1. Ventral scales with acute, tapering, lanceolate or linear appendages, usually purplish (Pl. 17, fig. 2); smaller species, less than 8 mm wide and 3 cm long, usually with margins of plant purplish 4

4. Pores simple, with a circular opening (Pl. 17, fig. 1) 5

5. Dorsal epidermis with thin walls, lacking trigones (Pl. 16, fig. 7); pores surrounded by 1-2 circles of cells; very small species, mostly less than 4 mm wide x 2 cm long 6

6. Dorsal epidermis delicate, rupturing and becoming fissured; pores becoming elongate, elliptical openings; ventral scales small, little or not purplish, scarcely imbricate ..... *Mannia* (*rupestris*)

6. Dorsal epidermis firm, persistent; pores remaining nearly circular; ventral scales blackish-purple, large, imbricate ..... *Asterella*

5. Dorsal epidermis with walls thickened at angles, usually strongly so (Pl. 17, fig. 1); pores usually surrounded by 3-5 concentric circles of cells (Pl. 17, fig. 1); moderate sized species 4-8 mm wide x 2-3 cm long ..... *Reboulia*

4. Pores compound: consisting of several superimposed circles of cells, the lower row of 4 large cells with a cruciate opening between them (Pl. 16, figs. 1-2); dorsal epidermis delicate, thin-walled ..... *Preissia*

Family REBOULIACEAE

I. ASTERELLA Beauv.

A. TENELLA (L.) Beauv.

Rare, very local. ONONDAGA CO.: on exceedingly marly moist soil at edge of brook, Clark Reservation, near Jamesville, *R. M. Schuster & W. Rader;* Stiles (Underwood & Cook, Hep. Amer. No. 44); Primrose Hill (Goodrich 1912, p. 24).

This small species is apparently very rare locally; intensive collecting in Tompkins, Cortland and Tioga counties has not resulted in its discovery there. The one locality discovered was composed of a remarkable associule on moist marl, with a coverage of 50-90%, varying locally, mainly of *Preissia quadrata, Conocephalum conicum,* the present species and a little *Riccardia pinguis.*

The small size (more the size of a *Riccia* than of *Reboulia*) and the very distinct dichotomous branching forming imperfect loose rosettes an inch or more across, the purple ventral scales and purple thallus-margins and the very strong, delightfully aromatic odor easily distinguish this species. The only other small species likely to be mistaken for *A. tenella,* is *Mannia fragrans* which differs in having a "white beard" of bleached ventral scales at the thallus apex. When fertile the conspicuous, lanceolately divided pseudoperianth surrounding each capsule is diagnostic.

II. MANNIA Corda (Grimaldia)

M. RUPESTRIS (Nees) Frye and Clark

Rare, local. SCHUYLER CO.: Havana (now Montour Falls) (reported by Peck, 19th Annual Report Univ. of the State of N. Y., 65, 1866, based on material collected by *E. G. Pickett;* cited by Evans, Bryologist 14: 85, 1911; the first report of the species from North America, according to Evans); Watkins Glen, June 1946, discharging spores, *Schuster.* ONONDAGA CO.: Marcellus, on rocks (Goodrich 1912, p. 24); TOMPKINS CO.: Lick Brook, 1945, *Schuster,* material little and determination doubtful.[30]

This species is a decided calciphile, occurring on rather moist, thin, limy soil over shale and sandstone, occasionally on narrow ledges on calcareous cliffs in ravines, associated with *Gymnostomum curvirostrum.* The measured pH range of the species lies between 6.8 and 7.9 normally. At both the Watkins Glen and Lick Brook localities the species was associated with both *Gymnostomum curvirostrum* and *Lophozia* (*Leiocolea*) *badensis,* two decided calciphiles. The moisture requirements of this species are rather intermediate between those of *Preissa* and *Reboulia* but the species seems to prefer more sheltered localities than either of these genera.

The small size separates this species from all our other species of Marchantiales possessing carpocephala except *Asterella tenella;* the lack of a pseudoperianth at once separates the species from the latter. In the vegetative state, well-developed thalli can usually be determined because the delicate dorsal epidermis of the thallus generally becomes ruptured, the dorsal thallus

30 The writer has also collected material from Buttermilk Glen, Tompkins Co.; this material has been lost so the citation is omitted above.

surface thus appearing irregularly lacunose much as in various species of *Riccia;* this characteristic separates it at once from our other Marchantiales with carpocephala, which all have a persistent dorsal epidermis that does not disintegrate. The virtually unlobed, hemispherical carpocephala are characteristic (Pl. 16, figs. 6, 7).

III. REBOULIA Raddi

R. HEMISPHAERICA (L.) Raddi

Frequent locally. TOMPKINS CO.: Coy Glen; Sixmile Creek Ravine; Sixhundred Ravine; Enfield Glen; Buttermilk Glen; Lick Brook; Old Buttermilk Glen; Taughannock; McKinney's Twin Glens; Renwick Brook; Fall Creek; Cascadilla Ravine. SCHUYLER CO.: Watkins Glen. ONONDAGA CO.: Jamesville Road (Goodrich 1912, p. 21); "Onondaga County" (Underwood & Cook, Hep. Amer. No. 22). MADISON CO.: Chittenango Falls.

A decided calciphile but also able to compete successfully under circumneutral and weakly acid conditions. Locally limited in occurrence to moderately dry vertical ravine-walls, occurring in the crevices, on thin soil but apparently rarely on the bare rock. Much less meso-hygrophytic than *P. quadrata* and often occurring on quite dry ravine-walls where it may dry up in summer, the thallus margins becoming strongly incurved. *Radula complanata* is a commonly associated hepatic, but usually grows in nearby areas on the rock itself, where it may grow with *Cololejeunea* and *Lejeunea cavifolia.*

The deeply, mostly 5-lobed female receptacles (Pl. 17, fig. 6) differentiate this species; when sterile the very inconspicuous, non-protuberant, simple pores separate it from *Preissia* the only other local species with moderately large thalli (1 cm wide or wider) that has the thallus-margin and ventral scales purple-pigmented. If a small portion of the dorsal epidermis is removed it will be seen that the cells are strongly thickened in the angles (Pl. 17, fig. 1), a characteristic which never occurs in any of our other Marchantiales. The pores are simple, unlike in *Preissia.*

Family MARCHANTIACEAE

I. LUNULARIA (Mich.) Adans.

L. CRUCIATA (L.) Dumort.

ONONDAGA CO.: Riegal Woods (Goodrich 1912, p. 23) evidently an erroneous record, since the species does not occur in "woods" this far north; Syracuse (Underwood & Cook, Hep. Amer. No. 64).

Occurring in greenhouses, probably to be found in all large commercial establishments in central and western New York; the following only definite records: TOMPKINS CO.: Botany Greenhouses, 1944-45, *Schuster;* Sage College Greenhouses, 1917 (now torn down); both on Cornell University campus. ERIE CO.: Conservatories, Buffalo (Day, 1882, p. 165).

The occurrence in greenhouses, as well as the unique, half-moon shaped, crescentic gemmae-receptacles adequately differentiate this species.

II. MARCHANTIA (March. f.) L.

M. POLYMORPHA L.

Abundant and widely distributed. TOMPKINS Co.: Fall Creek; Coy Glen; Cascadilla Ravine; Sixmile Creek; Enfield Glen; Lick Brook; Sixhundred Ravine; Swampy area 3 miles s.w. of Dryden; McLean Bogs; McKinney's Twin Glens; Esty Glen; Buttermilk Glen; Old Buttermilk Glen. LIVINGSTON Co.: Caledonia Fish Hatchery. MONROE Co.: Irondequoit Bay. MADISON Co.: Chittenango Falls. ONONDAGA Co.: Clark Reservation, near Jamesville. ALLEGANY Co.: Alma Hill. GENESEE Co.: near Bergen Swamp. ONTARIO Co.: Briggs Gully, Richmond. ERIE Co.: Buffalo and vicinity (Day 1882, p. 165). CATTARAUGUS Co.: St. Bonaventure; Four Mile Road, Allegany; Pumpkin Hollow, Five Mile Road, Allegany; Beehunter Creek, Allegany State Park; South Branch of Cattaraugus Creek, Gowanda (Boehner 1943, p. 15).

A species occurring almost exclusively in the ravines on moist shale and sandstone, or in marly places, on springy slopes. Occurring under a wide variety of conditions but apparently rare on the more acid substrata and rarely occurring on substrata rich in organic matter, differing thus from *Conocephalum* which grows equally well on organic and inorganic substrata. The limited tolerance for organic substrata nearly eliminates it from swamps and marshy areas where it is replaced almost completely by *Conocephalum*. Exceptionally occurring submerged in 3-6 inches of calcareous water in a form with vestigial pores as at Bergen Swamp.

The much darker green color, with the aereoles less strongly indicated and smaller in size, as well as the total absence of any odor, separates this species from *Conocephalum* with which it frequently grows. These two are our largest species, together with *Lunularia*, and can be told from all other genera by the absence of any extensive purple pigmentation of the ventral scales and the thallus margin. The cup-like gemmae cups always occur and adequately differentiate the species from all other genera. In totally sterile material, the compound pores together with the large size are diagnostic.

III. CONOCEPHALUM Web.

C. CONICUM (L.) Dumort.

Abundant and very widespread. TOMPKINS Co.: Fall Creek; Sixmile Creek; Sixhundred Ravine; Coy Glen; Cascadilla Creek; Lick Brook; Buttermilk Glen; Old Buttermilk Ravine; Woodwardia Bog; McLean Bogs; Malloryville Bog; 3 miles s.w. of Dryden; Ringwood; Headwaters Swamp; Michigan Hollow Swamp; Shurger Glen. CATTARAUGUS Co.: "very common" (Boehner 1943, p. 15). ONTARIO Co.: Briggs Gully, Richmond. WYOMING Co.: Letchworth Park (Boehner 1943, p. 15). TIOGA Co.: Southern parts of Headwaters Swamp. CORTLAND Co.: Beaver Brook. MADISON Co.: Chittenango Falls. SCHUYLER Co.: Watkins Glen. ONONDAGA Co.: Clark Reservation, near Jamesville; Howlett Gorge (Goodrich 1912, p. 24); Kirkville (Underwood & Cook, Hep. Amer. No. 3). MONROE Co.: Irondequoit Bay. SENECA Co.: Junius Bogs, nearby. CHEMUNG Co.: Southwest corner of county; Veteran. STEUBEN Co.: Waneta Lake. ONEIDA Co.: Taberg (Underwood & Cook, Hep. Amer., No. 3, in part). GENESEE Co.: Bergen Swamp. ERIE Co.: Goat Is., Niagara Falls (Day 1882, p. 165). Many more records available.

The most abundant and widely distributed of the thallose Hepaticae. Occurring under conditions of extreme alkalinity to decided acidity (as on very rotten logs), in ravines, on calcareous talus-slopes on cliff-walls, on

ledges, on marly banks, in swampy woods, on humus-covered banks and along paths, in acid, often inundated swamps. In general, meso-hygrophytic and with a well-defined tolerance if not preference, for limy substrates.

The very large size (1.5-2 cm wide, to 20 cm long), very distinct yellowish-green color, large, strongly defined areolae, absence of gemmae and absence of purple pigmentation as well as the decided aromatic odor easily distinguish this species when sterile. This (and *Lunularia*) is our only species possessing both simple pores and ventral scales with rounded, kidney-shaped appendages (Pl. 16, fig. 3). The conical carpocephala (Pl. 16, fig. 4) are diagnostic.

IV. PREISSIA Corda

P. QUADRATA (Scop.) Nees

Frequent locally. TOMPKINS CO.: Fall Creek Ravine; Sixmile Creek Ravine; Lick Brook; Buttermilk Glen; Enfield Glen; Coy Glen (Apr. 1903, *Jackson*). CAYUGA CO.: Paines Creek near Aurora. SCHUYLER CO.: Watkins Glen. MONROE CO.: calcareous ditch near Bergen Swamp. MADISON CO.: Chittenango Falls. ONONDAGA CO.: limey ditch-sides of Clark Reservation, near Jamesville; Jamesville Road (Goodrich 1912, p. 24); Marcellus, *Underwood*, 1885; Kirkwood (Underwood & Cook, Hep. Amer. No. 167, as *Cyatophora quadrata*). ONEIDA CO.: Taberg. ERIE CO.: Niagara Falls, near the American staircase (Day 1882, p. 165). CATTARAUGUS CO.: South Branch of Cattaraugus Creek, Gowanda (Boehner 1943, p. 15). WYOMING CO.: Letchworth Park (Boehner 1943, p. 15).

Locally much limited in occurrence because of its dependence on lime in the substratum and because of its rather hygrophytic tendencies. Occurring on two distinct types of substratum locally: on wet ravine walls, often on dripping ledges, with such species as *Lobelia Kalmii, Primulla mistassinica* and *Pinguicula vulgaris* and the Hepaticae *L.* (*Leiocolea*) *badensis, Riccardia pinguis, Pellia fabbroniana, Scapania mucronata,* etc.; and on the edges of calcareous ditches and springs as at Bergen and in Clark Reservation in Onondaga County. At Bergen it was abundant, with *Conocephalum* and *Marchantia* in a calcareous spring and there grew up fence-posts close-by, the only occurrence noted on an organic substratum; to be explained because the mats by capillary action, kept the uppermost plants saturated with calcareous water. At Clark Reservation, it formed an associule with *C. conicum* and *Asterella* and a little *Riccardia pinguis,* on white, exceedingly marly, heavy soil, which covered from 50-60% of the surface, locally to 90%, with the *Preissia* the dominant species. On ravine walls almost invariably associated with the moss *Gymnostomum curvirostrum,* equally calciphilous in nature; these two are the invading species of denuded, wet vertical cliffs.

This is our only species with the thallus deeply purple pigmented beneath and with the male receptacles elevated on a stalked receptacle. When sterile the meso-hygrophytic and decided calciphilous preferendum as well as the distinctly areolate thallus and absence of gemmae distinguish it. Most likely to be mistaken for *Reboulia;* when sterile the presence of swollen, elevated, whitish compound pores (Pl. 16, figs. 1, 2), easily differentiate it from *Reboulia* which also is moderate in size (less than 3 cm long and 8-9 mm wide) but has the pores simple, very inconspicuous, not elevated. The epidermal cells (Pl. 16, figs. 1, 2) are also thin-walled with the angles never thickened, unlike *Reboulia.*

Family RICCIACEAE

I. RICCIOCARPUS Corda

R. NATANS (L.) Corda

Frequent. TOMPKINS Co.: Inlet Marshes and Ithaca Flats, *var. coll.;* Headwaters Swamp, near West Danby, *R. M. & O. M. Schuster;* Michigan Hollow Swamp, *Rowlee,* 1893; Sapsucker Woods, Lansing, *R. M. Schuster, A. H. Wright, Ann Dunham;* Fir Tree Swamp near Freeville; south of Slaterville Swamp. SENECA Co.: Ovid (Nathan W. Folwell Herbarium, collected in 1831-1832; the oldest record of a hepatic from our area). ONONDAGA Co.: Onondaga Valley Road and near Salina (Goodrich 1912, p. 24). MONROE Co.: Greece, *R. M. & O. M. Schuster.* CAYUGA Co.: Owasco Lake. CHEMUNG Co.: *fide* S. J. Smith. WAYNE Co.: Sodus (Underwood & Cook, Hep. Amer. No. 1). CORTLAND Co.: Chicago Bog, near South Cortland, *Cipperly, 1902, Schuster, 1944;* Muddy Pond, Lower Labrador Valley, Truxton. *Wiegand;* Chicago Crossing near Cortland Marl Bogs; Turtle Pond, Truxton, *Wiegand,* 1892. ERIE Co.: Burnt Ship Bay, Grand Is., Niagara R. (Day 1882, p. 15). CATTARUGUS Co.: Bonaventure (Boehner 1943, p. 15).

An aquatic species of circumneutral or somewhat calcareous waters, occurring in shallow, still waters, with *Lemna species, Spirodela, Wolffia* or occasionally stranded on the shore when the water is low.

The habitat as well as the dense, stiff, sword-like, purple ventral scales adequately differentiate this species. From *Riccia fluitans,* the only other species that may occur with it, it differs in the broad thallus, the presence of ventral scales and the floating habitat.

II. RICCIA L.

KEY TO SPECIES[31]

1. Photosynthetic tissue loose, separated by more or less widely polyhedral air-chambers, the walls between these chambers only 1 cell thick (in *frostii* sometimes more compact, but not with narrow vertical canals throughout); ventral scales absent or obsolete 2
2. Aquatic species, occasionally stranded along shore; thalli very slender, linear, the segments less than 1.0 mm wide ..... *R. fluitans*
2. Terrestrial species, attached to the ground by rhizoids; thallus-segments not narrowly linear, more than 1.5 mm wide (Pl. 17, fig. 3) 3
3. Spores areolate on outer face at least, often over 65 μ long (Pl. 17, fig. 4); sections of thallus mostly 2.5-4 times as wide as thick; monoecious 4
4. Areolate of spore 10-30 μ wide on outer face (Pl. 17, fig. 4); chief thallus-segments 1.3-2.5 mm wide; dorsal surface soon spongiose or lacunose; terminal segments subquadrate-obovate to obcordate; dorsal groove poorly defined except near apex (Pl. 17, fig. 3) ..... *R. crystallina*
4. Areolae of spore 8-13 μ wide on outer face; chief thallus-segments 0.75-1.5 wide; dorsal surface with persistent, smooth epidermis (rarely spongiose-alveolate with age); terminal segments mostly oblong or elliptic; usually with wide, rather well-defined, shallow dorsal groove ..... (*R. sullivantii*)
3. Spores with short, delicate ridges that rarely anastomose, less than 65 μ in longer diameter (Pl. 17, fig. 5); dioecious; sections of thallus 1.5-3 times as

31 One species (*R. sullivantii*) is included in the key, since it occurs immediately south of us in western Pennsylvania, and certainly occurs in our area; *R. dunellii* (evidently in error for *R. donellii*) has been reported from Onondaga Co. by Goodrich 1912, p. 24, on the authority of Underwood; this is certainly an erroneous report since the species is Lower Austral and subtropical in distribution; hence the species is omitted from further mention.

wide as high; dorsal groove obsolete except at apex; dorsal surface soon becoming spongiose ..... *R. frostii*

1. Photosynthetic tissue compact, with narrow vertical or subvertical canal-like air-chambers (at times becoming polyhedral near margins); spores areolate to alveolate, over 65 μ in longer diameter 5

5. Median dorsal groove narrow and acute, the dorsal surface minutely, regularly, compactly reticulate ..... *R. sorocarpa*

5. Median dorsal groove obtuse, broad, usually a third or more the width of the thallus, the dorsal surface somewhat obscurely reticulate ..... *R. arvensis*

R. SOROCARPA Bisch.

Rare, doubtfully to be accredited to our flora. ERIE CO.: Forest Lawn Cemetery, Buffalo (Day 1882, p. 165).

The above record dates back to 1882 and is on the authority of Peck or Clinton. The possibilities of erroneous determination are not to be ruled out though the species is fairly easy to determine.

The large spores, mostly over 70 μ long, and the very narrow, acute dorsal sulcus together with the compact thallus, not spongiose and not lacunose, will serve to identify this species.

R. ARVENSIS Aust. (BIFURCA Hoffm.)

Rare. TOMPKINS CO.: Sixmile Creek, at edges of the lower reservoir, *I. Garber*, 1940; with good spores. CATTARAUGUS CO.: "moist banks of creeks, moist soil on Campus (Bonaventure College), etc." (Boehner 1943, p. 15).

Occurring under rather similar conditions as most of our species — moist, alluvial soils, in wet fields on open soil, etc., and at the margins of ponds and lakes.

The large spores, 70-110 μ in longer diameter, with the outer face with areolae 6-15 μ wide, distinguish this species; it is our only form with very compact assimilative tissue, and with a very distinct, broad median furrow (usually a third or more of the width of the thallus-segment).

R. FROSTII Aust.

Rare. MONROE CO.: Genesee Falls at Rochester.

On moist loamy soil and alluvial, silty river deposits; apparently rare in our area and with lime preference not known.

The small spores (under 65 μ), bearing short, delicate ridges (Pl. 17, fig. 5), rather than bearing areolae, easily distinguish this species from all others in our region; the thallus differs in being relatively narrower than *sullivantii* and *crystallina*, in section.

R. CRYSTALLINA L.

Rare. ONONDAGA CO.: Mud Lock (Goodrich 1912, p. 24), TOMPKINS CO.: Ithaca (Atkinson); *fide* Frye & Clark, 1937, p. 36.

The generally more robust, wider terminal segments of the thalli (Pl. 17, fig. 3), and the early rupture and disintegration of the epidermis (resulting in a spongiose dorsal surface of all but the youngest parts of the thallus) as

well as the much coarser often incomplete areolae of the spores (Pl. 17, fig. 4), separate this species from the closely related *R. sullivantii.*

(R. SULLIVANTII Aust.

Unreported from our area as yet, but occurring in McKean County (western Pennsylvania) immediately adjoining our borders and certainly to be found eventually).

R. FLUITANS L.

Infrequent. TOMPKINS CO.: Ithaca Flats, and along the Inlet, *var. coll.;* Dryden Lake, *B. Brown & W. C. Muenscher.* MONROE CO.: Greece, *R. M. & O. M. Schuster;* Irondequoit Bay, *Clausen & Hinkey;* Bullhead Pond, Township of Perinton, *Clausen & Hinkey.* SENECA CO.: south of the middle Junius Sphagnum Bog, *R. M. & Erwin Schuster.* ONONDAGA CO.: near Salina (Goodrich 1912, p. 24). ERIE CO.: Burnt Ship Bay, Grand Is., Niagara R. (Day 1882, p. 165). CATTARAUGUS CO.: Bonaventure (Boehner 1943, p. 15).

Probably more frequent than the above records indicate, but frequently overlooked. Generally occurring "floating" beneath the surface of the water but occasionally growing stranded, often with *Ricciocarpus.* Commonly found with *Utricularia vulgaris* and *Ceratophyllum.*

To be separated from all other thallose forms by the linear, often dichotomizing thallus, lacking rhizoids and ventral scales; furthermore, our only species growing suspended in water.

Anthocerotales

Family ANTHOCEROTACEAE

KEY TO GENERA

1. Capsules erect, filiform, sheathed for less than ¼ their length by the involucres usually (Pl. 18, figs. 8, 12), the capsules over 5 mm long; pseudoelaters not similar in size and form to the spores (Pl. 18, figs. 4-5, 9-10) ..... *Anthoceros*

1. Capsules horizontal or nearly, enclosed until maturity by the involucres of the gametophyte (Pl. 18, fig. 7); capsules less than 3 mm long; pseudoelaters similar in form and size to spores (Pl. 18, fig. 6) ..... *Notothylas*

I. ANTHOCEROS L.

KEY TO SPECIES

1. Spores yellow, granular-papillate; thalli flat and smooth, dark green, without lacunae in cross-section, larger, forming rosettes 15-25 mm in diam.; thallus-lobes few, broad, short, oblong (Pl. 18, fig. 12) ..... *A. laevis*

1. Spores black; thallus light green, with lacunae in cross-section, smaller, 4-10 (12) mm in diameter; thallus-lobes many, the lobes again with small, obcuneate or rectangular lobes, appearing somewhat crispate (Pl. 18, fig. 8) 2

2. Pseudoelaters well-developed (Pl. 18, fig. 10) of 1-5 elongate cells (2-10 times as long as wide); spores 30-50 μ, the outer face with 75-125 sharply spinose or papillose teeth, 3μ high or higher, the inner face foveolate-reticulate, lacking spines or papillae (Pl. 18, fig. 9); capsules when mature 15-50 mm high (Pl. 18, fig. 8) 3

3. Thalli but little crispate, moderately lobed and divided at margins, and lacking dorsal lamellae (rarely a very few); pseudoelaters mostly 1-2 cells long (rarely a few 3-celled), rarely as much as 90 μ long ..... *A. punctatus*

3. Thalli strongly crispate, densely divided at margins into narrow segments, dorsally with some to numerous lamellae (Pl. 18, fig. 8); pseudoelaters with some at least 3-5 cells long, often over 100 μ long (Pl. 18, fig. 10) ..... *A. crispulus*

2. Pseudoelaters rudimentary and inconspicuous (Pl. 18, fig. 4), of single cells that are about as broad as long (occasionally adhering and forming catenations, but never truly several-celled); spores 48-65 μ with both outer and inner faces similarly sculptured, muricate-tuberlate or with short, blunt papillae (Pl. 18, fig. 5); capsules when mature with rigid brittle valves, 3-8 mm high, often breaking at maturity ..... *A. macounii*

A. LAEVIS L.

Frequent locally, widely distributed. CATTARAUGUS CO.: Bonaventure; South Branch of Cattaraugus Creek, Gowanda; Martiny Rocks (Boehner 1943, p. 15). TOMPKINS CO.: Coy Glen, *R. M. & O. M. Schuster;* Enfield Glen, *R. M. & O. M. Schuster;* McGowans Woods near Ithaca, *Cipperly, Durant,* etc.; Varna, *Schuster;* 2-3 miles southwest of Dryden, *R. M. & O. M. Schuster;* headwaters of Sixmile Creek Ravine, *R. M. & O. M. Schuster;* Old Buttermilk Ravine, *Schuster;* southwest corner of Cayuga Lake, *Nanz;* West Hill, south of Coy Glen, *R. M. & O. M. Schuster.* TIOGA CO.: abundant in hills ¼ mile west of Richford, in many places; 2-3 miles east of Caroline, *R. M. & O. M. Schuster.* CORTLAND CO.: Morris Dam, Kenney Creek Valley, Truxton, *Wiegand.* SENECA CO.: path in woods near Junius Bogs, *R. M. & Erwin Schuster.* ONTARIO CO.: Briggs Gully, Richmond, *Schuster.*

Occurring in abundance on many of the shaded-to-rather-exposed, loamy or clayey, moist-to-wet banks of our area; more rarely (as at Briggs Gully), in crevices of wet shale talus, or over thin clayey soil over such talus, or on alluvial, sandy soil in ravines (as at Coy Glen and Enfield Glen). Usually occurring with *Blasia* and forming a definite union with that, *A. crispulus, Pellia epiphylla,* and more occasionally, *Fossombronia wondraczekii* and *Riccardia pinguis.* On alluvial soils or at the edges of shaded, loamy paths, occurring occasionally with *Notothylas* as at Enfield and Sixmile Creeks. With little tolerance for lime and absent in the more decidedly calcareous areas but a common species in the plateau region on the more subcalcareous or non-calcareous soils and shales.

The dark green thallus with broad, entire lobes, generally quite flat (Pl. 18, fig. 12), and the yellow spores, separate this species from all others.

(ANTHOCEROS RETICULATUS Steph.

Very doubtfully present in our flora. CATTARAUGUS CO.: *fide* Boehner 1943, p. 15. The specimen in question was determined by L. Clark, and I have not been able to examine it.

This species has not been reported elsewhere from the northeastern states; its presence in Cattaraugus County would be a most astonishing range extension. Until the record can be confirmed it seems best not to include the species either in the keys or text.)

A. PUNCTATUS L.

Infrequent or scarce locally. TOMPKINS CO.: Sixmile Creek Ravine, *fide* Andrews 1926; Old Buttermilk Ravine, *Durand, 1903, fide* Andrews 1926; Buttermilk Ravine below Tremans Lake, *R. M. & O. M. Schuster;* near entrance to Enfield Glen, *Kauffman,* 1902, *fide* Andrews 1926. TIOGA CO.: abundant in the hills 2-4 miles southeast of Caroline and about 1 mile west of Richford, *R. M. & O. M. Schuster.* ONONDAGA CO.: Syracuse (Underwood & Cook, Hep. Amer. No. 82).32

This species has been confused frequently with *A. crispulus* and it is questionable how well separated the two are, as regards their species characters. Field study indicates that locally at least, *A. punctatus* is a more gregarious plant, frequently growing in rather large mats while *A. crispulus* generally occurs as distinct, separated thalli, rarely occurring in any quantity. Several of the above records may possibly belong to *crispulus.*

A. punctatus occurs under identical conditions as *A. laevis* but rarely forms *Massen-vegetation* in the manner that the latter does. It usually occurs in relatively small quantity and when growing with *A. laevis* generally appears to be an accessory species, unable to compete too successfully against *laevis.*

The much more slender, thread-like, blackish sporophytes of this species and the next, as well as the more strongly divided thallus, easily separate *punctatus* and *crispulus* from *laevis,* even in the field. The present species differs from crispulus in having the dorsal surface relatively smooth with no or only very rare dorsal lamellate outgrowths, and in having the thallus somewhat less crispate, less divided; the pseudo-elaters furthermore, are more reduced, and rarely does an individual one reach 3 cells in length. The spores are virtually identical with those of *crispulus* (Pl. 18, fig. 9).

A. CRISPULUS (Mont.) Douin

Rather rare locally? TOMPKINS CO.: on loamy, wet bank near Varna, *Schuster,* 1945; Sixmile Creek, on shaded loamy path, *Schuster;* Coy Glen, on wet loamy bank, *R. M. & O. M. Schuster;* shaded, moist, loamy wagon-road 2 miles south of Dryden, *R. M. & O. M. Schuster.* CATTARAUGUS CO.: "common"; South Branch of Cattaraugus Creek, Gowanda; Bonaventure; field, etc. (Boehner 1943, p. 15). ONONDAGA CO.: Syracuse (Underwood & Cook, Hep. Amer. No. 82, in part).33

This species generally occurs together with *A. laevis* and *Blasia* and occasionally with *Fossombronia wondraczekii, Plectocolea crenulata* and *Notothylas orbicularis.* Usually occurring as separated, isolated, solitary thalli, often but a very few in any one locality; because of this, evidently heretofore overlooked; its real abundance not yet ascertained. Apparently with a rather low tolerance for lime and occurring under distinctly more shaded conditions than those under which *A. punctatus* and *laevis* often occur, but able to exist under quite mesophytic conditions.

Differing from our other species in the presence of usually numerous

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32 The specimen of this number examined had pseudoelaters mostly 2-5 cells long, and some dorsal lamellae of the thallus; therefore at least part of the material issued in this number should be called *crispulus.*

33 See discussion under *A. punctatus,* under which name this number was issued.

dorsal lamellate outgrowths of the thallus-surface; these together with the finely divided margins of the plant give it a decidedly "dusty," irregular appearance to the naked eye; the rosettes are usually very distinct, nearly circular, and rarely over 12 mm in diameter. The often elongate pseudo-elaters may be 5-6 cells long but the majority are 1-3 cells in length.

A. MACOUNII Howe

Very rare locally. TIOGA CO.: loamy bank along hillside, shaded road, 1 mile west of Richford, *R. M. & O. M. Schuster*, 1943.

This species is much more distinctly northern than our other forms, the shorter capsules being evidently an adaptation towards a shorter growing season. This and the record for Connecticut, are the southernmost records for the species.

The single collection consisted of only a small patch of about a dozen rosettes that were growing with *A. laevis* and *punctatus*, accompanied by *Pellia epiphylla*, *Blasia* and *Fossombronia wondraczekii*. At first the material was believed to represent an atypical form of *punctatus* but the dehiscing capsules failed to elongate after about a month of culturing when the plant finally died. The short rigid valves, less than a fourth of an inch high, the black spores and the rudimentary pseudoelaters (Pl. 18, fig. 4), left scarcely any doubt but that the present species was at hand. The specimen unfortunately was not preserved. The spores (Pl. 18, fig. 5) of this species are larger than those of our other species and differ from them in that the inner surface of the spores is muriculate.

II. NOTOTHYLAS Sulliv.

N. ORBICULARIS (Schwein.) Sulliv.

Rare locally. TOMPKINS CO.: moist ground at base of rocks, southwest Corner of Cayuga Lake, Ithaca, *Atkinson* 1893; Enfield Glen, on moist, rather shaded, alluvial sandy-silty deposits in the ravine, *R. M. & O. M. Schuster*, 1944; Sixmile Creek, along shaded, moist, loamy-gravelly path, *Schuster*, 1945. CATTARAUGUS CO.: "field at Chamberlain's Bog, Steamburg"; Bonaventure (Boehner 1943, p. 15).

This species occurs more often on alluvial soils, often at the edges or on the flood-plains of streams or lakes, than do the species of *Anthoceros*, though it may occur together with *Anthoceros* (with *A. laevis* at Enfield; with *A. laevis* and *crispulus* at Sixmile Creek). Occurring always in very small quantities locally; at Enfield Glen about 10 rosettes were found, at Sixmile Creek, about 20-24.

The very short, spindle-shaped horizontal capsules surrounded until maturity by the gametophytic involucre (Pl. 18, fig. 7), and the small size of the rosettes (rarely as much as 8 mm across), easily distinguish this genus from *Anthoceros*. Confusion with other genera is scarcely possible. This species also differs from *Anthoceros* in the subspherical, rudimentary pseudoelaters (Pl. 18, fig. 6) that are similar to the spores in form but differ in being a little larger and showing irregular internal bands of thickening.

PART II.

ECOLOGICAL AND PHYTOGEOGRAPHICAL OBSERVATIONS

The Region Treated

Central and western New York are here arbitrarily taken to comprise that part of the state west of about 75°30′ and south of about 43°30′ latitude. The marginal regions have been only haphazardly collected. Except for a very small area in Allegany and Cattaraugus counties near the Pennsylvania border, which exhibits remnants of a decidedly "Canadian" flora, and for a narrow strip along Lakes Erie and Ontario, running east to about Monroe County, which is "Upper Austral" in facies, our entire region belongs to the "Transition" Zone.[34] The northern part of the region is flat, with very low hills, drumlins and irregular glacial dumping, resulting in many swamps and bogs; this area has been called the Ontario-Erie Basin of New York by Forbes (1926) while Fenneman (1938) called it the Eastern Lake Section of the Interior Lowlands, of the Central Plains Province. The southern two-thirds of our region includes what Forbes has called the Appalachian region, and Fenneman the Eastern New York section of the Appalachian Plateau. These two areas differ considerably in the nature of the vascular fora. The hepatic flora is perhaps not as strongly differentiated however, but many "Canadian" species found in the Plateau region (such as *Scapania mucronata, Tritomaria exsectiformis, Gymnocolea inflata, Anastrophyllum* (*Sphenolobus*) *minutus, Lophozia excisa, Anastrophyllum michauxii* and *Bazzania denudata)* are absent on the Ontario-Erie Basin while a number of lowland forms, more common on the Coastal Plain and in the Mississippi Valley (as *Riccia*) occur apparently more frequently in the Ontario-Erie basin than in the Plateau region.

The differentiation into two floral regions can be explained much more satisfactorily on a basis of differences in topography (absence of cliffs and ledges in the Ontario-Erie Basin, etc.), and relative abundance of underlying calcareous rocks rather than on a basis of climate. An exception may be offered by the high hills of Allegany and Cattaraugus counties where the elevations appear to make possible the survival of Canadian forms (as *Lophozia attenuata, Bazzania tricrenata* and *Bazzania denudata*) which are absent elsewhere in our region.

For a more detailed discussion of a large part of the area treated, see Wiegand and Eames (1926), Appendix, pp. 435-448, and Zenkert (1934).

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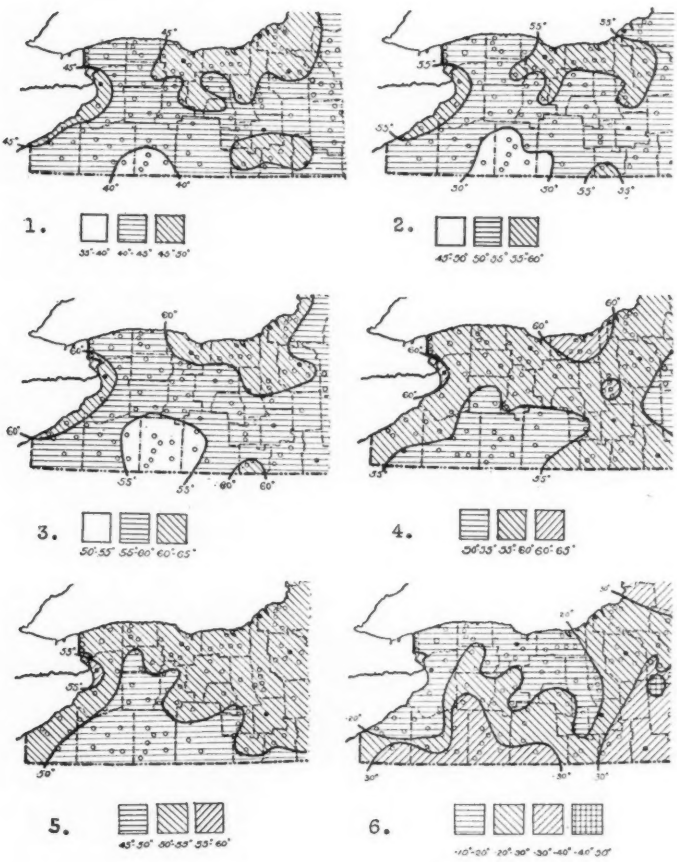
34 See Figures 1-9, where the temperature factors responsible for such a disposition are graphically portrayed. It will be noted that the area with a growing season of 100 days or less corresponds with the "Canadian" floral region while the area with a growing season about 165-170 days long or more approaches the "Upper Austral," with the intermediate area "Transition."

PHYSICAL AND GEOLOGICAL FEATURES

The elevation of the region varies from 246 feet at the edge of Lake Ontario, to somewhat over 2500 feet in Cattaraugus and Allegany counties. These differences in elevation make little difference in the nature of the hepatic flora, with the single exception of some of the high hills of Steuben,



Figs. 1-6. Climatic Maps (Courtesy N. Y. Agr. Expt. Sta.).—1. May mean minimum temperature. 2. June mean minimum temperature. 3. July mean minimum temperature. 4. August mean minimum temperature. 5. September mean minimum temperature. 6. Lowest temperature recorded. (From Mordoff, 1924).

Allegany and Cattaraugus counties, which support many "Canadian" plants (forming, in fact, the predominant hepatic flora, as at Rock City).

Since the underlying rocks often have a profound effect on the nature of the flora (directly in the case of saxicolous forms, and indirectly in the case of other species) insofar as they largely determine the nature of the soil the species inhabit, it is felt that a short discussion of the petrography as well as the physical features, is needed for a clear understanding of our flora.

The rocks of the entire region are Silurian-Devonian sedimentary rocks except the Oswego Sandstones (provided by a slight extension of the Upper Ordovician into the northeastern corner of the region treated) and limited Carboniferous outcrops near the summits of the hills in Allegany, Cattaraugus and Steuben counties.

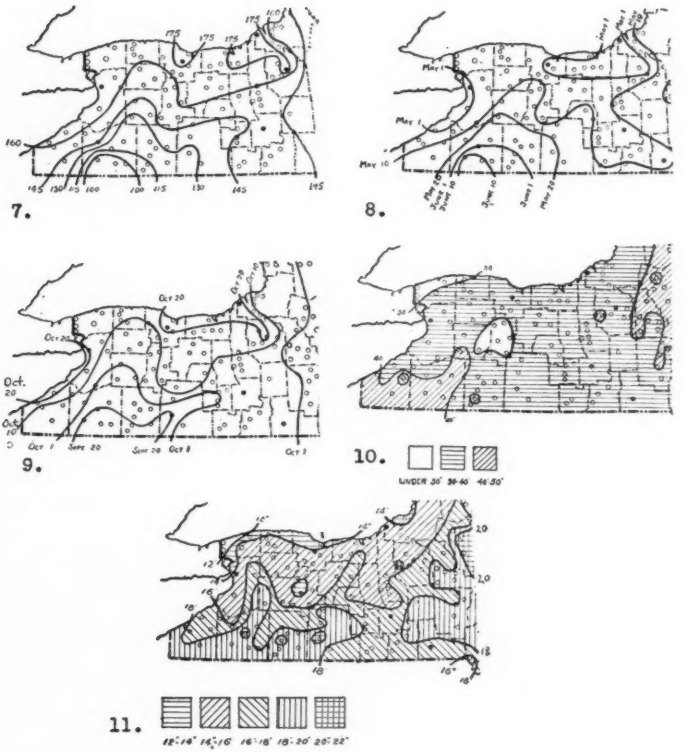
The whole region has been glaciated and the southern part has been peneplaned. The frequent deposition of calcareous glacial drift to the south of the region where outcrops of limestones and calcareous shales and sandstones commonly occur, has resulted in a largely calciphile flora even south of the Lower Devonian system. The dip of the rocks is gently to the south and for that reason the older rocks are exposed towards the north. They are exposed also in places to the south where the creeks and streams have cut deep gorges, frequently 250-350 feet deep or deeper.

That portion of the Ontario-Erie Basin along Lake Ontario consists of Silurian rocks (except for slight Ordovician outcrop) and comprises in the north a narrow strip of Lower Silurian (Medinan) outcrops. To the south of this again lies a narrow strip of Middle Silurian formations (the Clinton Beds and Lockport Dolomite) overlain southward by the Upper Silurian outcrops. The latter beds are very rich in limestone and calcareous shales; overlying them are extensive calcareous bogs and swamps featuring extensive stands of the calciphilous *Thuya*. This region is one of the most fascinating as regards the hepatic flora — marl bogs and swamps often occur almost side by side with acid *Sphagnum* bogs and support a rich and diversified flora.

All the rest of our region except the limited carboniferous exposures described below, consists of Devonian formations. This comprises fully three-fourths of central and western New York. The narrow glacial lakes running roughly north and south, called the Finger-Lakes, are characteristic of this region. To the north they barely enter the Ontario Plain and Silurian system; to the south they end in the relatively rolling, hilly country of the Appalachian Plateau. Post-glacial lowering of the waterlevel (a result of the gradual disappearance of the northern ice-block) of these lakes resulted in hanging creeks which cut deep gorges and usually end in one or several waterfalls shortly before they enter the lake valleys. These deep, post-glacial gorges and ravines undoubtedly support the richest and most diversified hepatic flora of the region. The Devonian formations lie almost entirely within the Appalachian Plateau, as defined by Forbes and Fenneman, except for a narrow strip along Lake Erie and near Buffalo, which forms the Erie Basin. This

Plateau region varies in elevation from about 800-900 feet in the north, to well over 2500 feet in the south, and has been peneplaned, with the hills formed by glacial dissection and subsequent erosion by the post-glacial streams and rivers.

The Devonian formations consist of a narrow strip of Lower Devonian rocks, not extending entirely across our region, composed mainly of limestone. Overlying this and exposed to the south, is a wider portion of the Middle Devonian of grit, limestone and shale. The southern three fourths of our region consists of Upper Devonian beds through which the ravines described



Figs. 7-11. Climatic Maps (Courtesy N. Y. Agr. Expt. Sta.).—7. Average length of growing season, in days. 8. Average date of last spring killing frost. 9. Averate date of first killing frost in fall. 10. Mean annual precipitation. 11. Mean precipitation for growing season (May 1-Sept. 30). (From Mordoff, 1924).

above cut; they include a thin layer of Tully limestone, of Genesee calcareous shales, and of Portage-Naples-Ithaca-Oneonta Beds, capped by the Chemung Sandstones near the southern limits of this area. These Upper Devonian beds are largely of alternating layers of sandstone and non-calcareous shales, mostly the latter. In the ravines however, enough local calcareous shale outcrops occur to result in a predominantly "calciphile" flora, except for the leached soils of the crests where an oxylophyte Vaccinium-Chestnut-Hickory flora frequently occurs.

Crossing the basins of the lakes near their southern borders, is a glacial moraine of considerable size, which, as well as the drumlin area of the Ontario Plain, supports many peat-bogs and small ponds, usually formed by irregular glacial dumping and damming of drainage valleys. These bogs and swamps form one of the most interesting features as regards the hepatic flora. Limited to these bogs are such species as *Mylia anomala, Cladopodiella fluitans, Cephaloziella elachista* and *Lophozia marchica.*

As has been mentioned, limited Carboniferous outcrops occur at the highest elevations near Olean and Rock City (Allegany and Cattaraugus counties). The Lower Carboniferous Cattaraugus beds consist largely of conglomerates while the even more restricted and limited outcrops of Upper Carboniferous Olean Conglomerate beds are capped by a thin layer of Sharon shale, the youngest of the formations of our area. The conglomerates of this area, consisting largely of cemented quartz pebbles, support a diversified and characteristically different flora than the rest of the region. Many species more common in acidic regions occur only here since the calcareous or subcalcareous nature of much of the rock to the north and the often calcareous glacial drift, appear to limit the occurrence of these species. The relatively high elevation (largely over 2000 feet in the hills) further tends to make the survival of a relatively boreal flora possible.

Much of the region except for the bogs and swamps (which have often been drained and reclaimed) and for some of the summits of the highest hills, is under cultivation. The steep, often precipitous ravines have been molested least by man and frequently have not even been lumbered. Many species appear to be rare now largely because of the activity of man. The hepatic flora of the Ontario and Erie basin has been largely obliterated; on the Plateau region, lumbering has wiped out many of the more tender species that do not "tolerate" much of the activities of man. The more interesting ravines have been made into State Parks and are gradually being depleted of much of their wild-life. Among the latter, many Hepaticae because of their sensitivity to the activity of man, are among the first to go. Therefore, the local distribution of many species has been given in full since the day is surely near when they will be absent from many of their former haunts.

GLACIATION AND ITS EFFECTS

All of central and western New York has been glaciated, excepting a small triangular area south of Salamanca, which is largely inclosed in Allegany State Park. Zenkert (1934) writing on vascular plants of the region states,

"Some rather striking physiographic and floral contrasts are presented by the unglaciated area of Allegany State Park, to the south of Salamanca. Not a single natural lake, pond, or true bog is to be found within the confines of the Park. Furthermore, the terminal moraine rather abruptly marks the limit of most of the northern vegetation, the flora of the Park area being notably deficient in boreal elements, particularly bog plants."

It should be stated however, that in the unglaciated area just east of Allegany Park at elevations of about 2400 feet, the hepatic flora is quite northern, indeed, including a higher percentage of northern forms than present elsewhere in central and western New York. The reason for this appears to be resolvable into two contributing factors, 1) the occurrence of quartz conglomerate or siliceous rocks that enable many members of the northern, acidic rock-loving *Lophozia* complex to exist, and 2) the higher elevation, resulting in a lower temperature and shorter growing season. Indeed, there is a difference of 60 days in the length of the growing season between the area directly north (near Buffalo) and directly west (near Chatauqua Lake), and the Rock City area and its environs.

The often largely "calciphilous" flora of our general area has already been noted, as also has its remarkable diversity. Zenkert (1934), writing on the vascular plants, eloquently gives some of the reasons for these facts, that apply equally well to the hepatic flora: "A region rejuvenated in its physical aspects emerged after the final retreat of the ice sheet. The freshness and richness of the commingled soil deposits,[35] the shore lines of lakes, large and small, and the morainic hills and ridges alternating with marsh depressions — this diversity of substratum and habitat induced a general migration of vegetation back northward and brought on a relatively rapid recolonization of the glaciated Tertiary. In their northward dispersal, not a few components of the sub-arctic flora found a congenial environment, particularly in the Allegany uplands.[36]

"Here the higher altitudes and slower run-off of the impounded waters, together with the lower rate of evaporation, favored the formation of peat bogs and the maintenance of conditions suitable to the development of northern

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35 Residual soils in unglaciated areas, as decomposition products of a weathering process extending much further back into geological time, have parted with their more soluble constituents, whereas glacial soils, relatively rich in lime, potash and phosphorus and subjected to a shorter process of weathering, have retained a larger proportion of their soluble mineral matter.

36 This last statement is rather misleading since the few truly subarctic vascular plants (*Primula mistassinica, Pinguicula vulgaris, Saxifraga aizooides*) for which the region is notable, and such northern hepatics as *Jungermannia caespiticia, Lophozia marchica, Lophozia rutheana, A. minutus* and their kin, are all plants existing more or less as disjuncts in our region, isolated in either deep, cold, perpetually moist ravines or in cold, equally disjunct *Sphagnum* bogs. It is therefore not a question of a congenial environment but rather a differential survival rate of individual colonies existing under conditions generally varying from suboptimal to optimal. The few populations existing or colonizing the coldest, deepest gorges and coldest bogs would survive longer than those existing under less subarctic conditions, and have indeed, survived in few cases to the present day.

plant forms. . . . Bogs in various stages of development, as well as smaller lakes, are still a characteristic feature of this upland country, and a diminished number of northern plant forms are still thriving there, largely as relics of the sub-arctic flora that migrated northward."

Another factor, not stressed by Zenkert is the formation of deep, cold, shaded gorges and ravines (largely in the upland country) as a result of glacial damming to the north, followed by swift recession of the water level when the northern ice-block disappeared, and the cutting of gorges by the hanging creeks that had been suddenly transformed from mature to young streams. These ravines offered shelter to an entirely different group of northern plants. In the ravines the mean annual temperature and growing season are both notably lower than in the surrounding country; furthermore, the ravines greatly increase the diversity of the terrain and offer shelter to plants *(Ptilidium cillare, Lophozia* spp., *Scapania mucronata, Mannia rupestris, Gymnocolea inflata,* etc.*)* that have not been able to survive elsewhere in our region.

The Ecological Factors

Before touching upon the synecology and microdistribution of Hepaticae, as well as their geographical distribution, it seems fitting to briefly emphasize the factors that determine the microdistribution of the various species locally.

With extended field study certain broad generalizations can be formulated, though such generalizations remain relatively barren and are always apt to contain subjective elements. Very little experimental data have accumulated and therefore it is difficult to present more than broad and often obvious generalizations.[37] The paucity of actual knowledge is due, in part, to the absence of the stimulus given the study of a group of plants that contains economically important species. Partly responsible also is the fact that the determination of species is often so difficult, the ecologist does not work with them. In addition, the difficulties that attend the culture of the species have been responsible in this regard.

The extrinsic factors that interoperate to circumscribe the distribution of the various species can be briefly classified as follows:

Atmospheric Factors

Temperature.—The effect of temperature, *per se,* is extremely difficult to evaluate since high temperature conditions are usually correlated with strong insolation, and low temperatures with weaker insolation, in locally limited niches. It is therefore quite impossible to keep the temperature factor (i.e., effects of infra-red and visible red waves) and light factor (effects of visible waves) separated. It is perhaps somewhat unnatural to do so, for our purposes, since those species with a high temperature preferendum (or toleration) are also generally those with a higher toleration for light and periodic desiccation. To what degree temperature is a critical factor in limiting distribution

37 For a review of the scant experimental work, see Davy de Virville, 1927. Buch (1922) also discusses critically the effect of the environment on the form of the species. There is even less known about the effect of the environment on the survival and reproduction of the species. See also Stern (1938) and Voth & Hamner (1940).

of a species locally, is therefore nearly unknown. The local species able to tolerate high daily temperatures are chiefly those belonging to the xerarch Pitch Pine and Oak-Hickory communities: *Cephaloziella rubella* and *byssacea, Lophozia bicrenata, Ptilidium pulcherrimum,* etc.—all morphologically well adapted to xeric conditions and able to produce secondary pigments capable of shutting out light of certain frequencies.

As regards macrodistribution, temperature has only a limited effect in a region with as narrow a latitudinal and altitudinal range as central and western New York. However, under several special conditions the local distribution of Hepaticae may be obviously influenced.

a. At elevations above 2000 feet (as in Steuben and Cattaraugus counties) some "Canadian Zone" or Subarctic-subalpine species are able to survive.[38] Among these are *Anastrophyllum minutus, A. michauxii, Lophozia longidens, L. gracilis, Scapania subalpina, S. cuspiduligera, Bazzania denudata* and *B. tricrenata.*

b. On north-facing sides of the ravines more or less disjunct northern species survive, perhaps also as relics of the glacial period, associated with such northern vascular species as *Primula mistassinica* and *Pinguicula vulgaris.* Among these are *Gymnocolea inflata, Tritomaria exsectiformis, Lophozia excisa, L. ventricosa, L. incisa, Jungermannia caespiticia, Scapania mucronata,* etc. The local differences in temperature between the surrounding countryside and the shaded, sheltered ravine-slopes is striking, especially on hot summer days. The northern facies of the hepatic flora of the ravines is perhaps largely due to the cooler temperatures prevailing there.

c. In cold bogs and swamps, especially above 1200 feet, other northern species survive, associated with remnants of the Northern Coniferous Forest Climax. Among these are *Cephaloziella subdentata, C. elachista, Lophozia porphyroleuca, L. marchica, L. rutheana, Harpanthus flotowianus, Mylia anomala, Calypogeia sphagnicola, Cladopodiella fluitans, etc.*

Although the first category listed above represents, in part at least, a true difference in macrodistribution based on general climatological differences, this scarcely holds for the latter two categories. These are based on microclimatological differences caused largely by differences in terrain but probably, in part at least, by the historical factor (glaciation and subsequent persistence of northern relics).

Moisture.—The general rainfall for the whole region is moderate (largely between 30 and 40 inches, see Figs. 10, 11). Varying moisture conditions of both the substratum and atmosphere are therefore essentially due to the microenvironment; they are of prime importance in the local differentiation of the

38 To what degree the occurrence of such Subarctic-subalpine species this far south, is due to historical factors, is not entirely clear. The apparent concentration of northern species in the Cattaraugus County region is resolvable into two main causal factors: lower temperatures and shorter growing season existing there (see Figs. 1-9), and lack of glaciation. Possibly the historical factor is here more significant.

hepatic flora. The nature of the forest covering influences the moisture conditions of the substratum, and also the humidity immediately above the substratum (which essentially has the greatest effect on the survival of the Hepaticae). The richness of the hepatic flora of the north-facing slopes of the ravines is in part due to the rather constant and often high moisture content of the substratum and perhaps slightly higher prevailing humidity. The cool, moist winds prevailing in the ravines, the result of cooling and saturation of any air entering them by the cold creek waters, appear to be of great importance in enabling the delicate northern species to survive.

The water-requirements of Hepaticae vary widely; the following may be cited as typical illustrations: *Ricciocarpus natans* and *Riccia fluitans* are hydrophytic; *Chiloscyphus pallescens* var. *fragilis* and *C. polyanthus* var. *rivularis* may be hydrophytic but are often merely hygrophytic. *Porella pinnata* is generally hygrophytic; *Preissia commutata, Lophozia marchica, Trichocolea tomentella* and other bog species are usually hygrophytes. The vast majority of our species however, are mesophytes, or xerophytes. *Bazzania trilobata, Jungermannia lanceolata, Blepharostoma trichophyllum* and *Lepidozia reptans* are typically all mesophytes. *Radula complanata, Lejeunea cavifolia, Frullania* spp., *Porella platyphylloidea* and *platyphylla* are typically xerophytes. Ochsner (1927) has suggested some bryophytes may be used, alone or correlated with vascular plants, as indicators of moisture conditions; local studies tend to support this suggestion but they also emphasize the fact that microdistribution may be the result not only of moisture but of moisture plus temperature and light conditions. Any one species appears able to survive under conditions of lesser moisture if either the temperature is lower or the light intensity less, or both; the inverse holds with equal validity. This would suggest that many Hepaticae can be used only as qualitative indicators of moisture conditions unless correction for temperature and light intensity is made. Furthermore, many Hepaticae are very ubiquitous as regards moisture conditions; *Scapania irrigua* locally varies in occurrence from hygric to xeric conditions in a very small area; many similar illustrations can be cited. Other species however, are very intolerant of wide variations in moisture largely because they appear unable to produce modifications that enable them to grow under widely different conditions. For instance, the apparent inability of *Lophozia marchica* and *mildeana* to produce secondary thickenings of the cell walls is usually correlated with an hygrophytic habitat; they are consistent hygrophytes, without any tolerance for conditions of intermittent moisture.

There is an interesting correlation between the occurrence of xerophytic (most common in the relatively exposed Oak-Chestnut Forest) and the mesophytic and hygrophytic forms (more predominant in the humus and wet ledge flora of the *Hemlock-Yellow Birch* Associes).

The tolerance of many species is quite great; for instance, I have found such species as *Bazzania trilobata* growing 7-8 feet above ground level on the bark of trees, and I have found the same species growing among *Sphagnum* tufts (Ringwood) in an open, sunny, swampy pool. It should be noted however, that the Lick Brook and Headwaters Swamp stations where the species

grew on bark, were in swampy, low depressions, or moist, shaded ravines where the humidity of the air was quite high.

However, most species have very narrow tolerances as regards moisture conditions and are unable to succeed on substrata more xeric or hygric than that on which they normally grow. This sensitivity to moisture may be illustrated by the following example. *Radula complanata,* an exceedingly common species in the ravines of central New York, is relatively rare elsewhere in our region. This species occurs perhaps most abundantly on vertical, somewhat moist-to-moderately-dry shale and sandstone cliffs or on isolated rocks and boulders but it is also abundant in ravines on bark. In non-ravine areas the species is virtually absent from the bark of the same species of trees. Two explanations suggest themselves, (a) the species is essentially an epipetric plant which is able to invade but unable to succeed or compete on bark as successfully as many mosses, lichens and *Frullania* (this hypothesis is perhaps partly true since in our region the species seems to fruit more abundantly when growing on somewhat moist rocks or on roots where the humidity is relatively high) i.e., the corticolous population is dependent upon a reservoir population on rocks to renew itself; (b) the species is limited largely to the ravine area because of its high humidity requirements. This latter hypothesis appears to be largely true since we find that the *Radula* occurs in swamps far away from ravines in central and western New York as at Woodwardia Bog, Headwaters Swamp, source of Sixmile Creek, McLean Bogs, Michigan Hollow Swamp, swampy area near Solon and McLean Bogs, etc. All these locations are depressed, wet and swampy regions where there is little wind and the humidity is relatively high. It is therefore justifiable to consider the limited distribution of the *Radula* as largely due to a lack of tolerance for very xeric conditions. It is well known that Hepaticae are able to utilize the moisture of the air when humidity conditions are relatively high. The factor of atmospheric moisture thus is essentially the controlling factor in the distribution of the plant.

It is of some interest that two other species of *Radula (R. obconica* and *R. tenax)* are reported by Sharp (1939) as occurring commonly on bark at high elevations in the Smokies. The strict limitation of these species to vertical sandstone and shale ledges, under relatively mesic conditions locally, might be misinterpreted as being due to an inability to grow on other substrata, i.e., to edaphic factors; the true explanation however, lies in the fact that rainfall and relative humidity in the Smokies are very much higher than in our region and therefore enable these two species to compete successfully on bark while they are entirely unable to invade bark in our region.[39]

An almost parallel case may be cited. *Frullania asagrayana* locally occurs on bark in swamps and bogs (Headwaters Swamp, Plymouth Bog, Waterman Swamp, etc.) which generally have a higher humidity than the less depressed regions surrounding them. This species appears to be almost entirely absent however, from the rest of our region except in the ravines where it occurs

39 See Billings and Drew (1938) for a discussion of the factors influencing the distribution of corticolous species.

chiefly on moist, shaded rocks with such mesophytes or mesoxerophytes as *Metzgeria conjugata, Radula complanata* and *Lejeunea cavifolia*; it is known from Sixmile Creek, Coy Glen, Enfield Glen, etc., as regards the ravines. The limiting factor in the distribution of this species again is the dependency on a meso-xerophytic habitat, irrespective to some degree, of the nature of the substratum.[39a]

Light.—In general, light is a most significant factor in determining micro-distribution of Hepaticae in any one region. The amplitude of light toleration of many species is very broad but generally it covers only a small segment of the total range of intensity existing in nature. Some species have an extraordinary range. *Conocephalum conicum* under rather moist conditions, may exist under light conditions approaching full sunlight (1/1) while it has been reported also from holes with a light intensity of only 1/400. However, such a range is exceptional and most species have relatively narrow amplitudes.

On the basis of light toleration (and/or prefrence) we may arbitarily separate our species into two groups:

LIGHT TOLERATING (Heliophile and "photophile")	LIGHT AVOIDING ("Sciaphile")
Ptilidium ciliare	*Calypogeia* spp.
Ptilidium pulcherrimum	*Cephalozia media, catenulata*
Nowellia curvifolia	*Trichocolea tomentella*
Lophozia bicrenata	*Anastrophyllum minutus*
Marchantia polymorpha	*Anastrophyllum hellerianus*
Preissia quadrata	*Lophozia badensis*
Cephaloziella spp.	*Geocalyx graveolans*
Gymnocolea inflata	*Scapania apiculata*
Cephalozia bicuspidata	*Scapania glaucocephala*
Jamesoniella autumnalis	*Cololejeunea biddlecomiae*
Lophozia porphyroleuca	*Metzgeria conjugata*
Lophozia barbata	*Metzgeria furcata*
Mylia anomala	*Riccardia latifrons*
Frullania spp.	*Riccardia sinuata*
Blasia pusilla	*Mannia rupestris*
Pellia epiphylla	*Pellia fabroniana*
Riccardia pinguis	*Moerkia flotoviana*
Riccia spp.	*Blepharostoma trichophyllum*
Ricciocarpus natans	*Bazzania denudata*
	Diplophyllum apiculatum

[39a] Even more rarely such generally lithophilous species as *Metzgeria conjugata* may occur on the bark of trees (as at the base of a yellow birch in Lick Brook ravine) where the site is one in which the atmospheric humidity is extremely high. The somewhat xeromorphic *Ptilidium pulcherrimum* also may occur on bark (Headwaters Swamp) though in regions with a rainfall as low as this, it is confined almost exclusively to decaying logs and humus. The most extreme case of this type known to me, is the occurrence of *Anastrophyllum* (*Crossocalyx*) *hellerianus* on the bark of a *Tsuga* at about 6-8 feet above the ground. This collection (Lick Brook) was taken from the deepest, most narrow, shaded, cool and humid portion of the ravine.

Brown (1948, p. 487) also reports such species as *Lophocolea heterophylla, Ptilidium pulcherrimum*, etc. as epiphytes in the gorges of central New York and from bogs in the same general region.

Our Hepaticae essentially consist of two large groups, (1) forms differentiated as regards structure of the plant body, and with reduced sporophytes such as the *Marchantiales* which are almost without exception light-loving forms, and (2) forms with delicate gametophytes and less reduced sporophytes, with a long seta, including the *Jungermanniales* which are essentially forms with low light requirements; indeed, usually they have but very low tolerances for light. Secondary adaptation of the *Jungermanniales* towards existence under conditions of intense light (generally correlated with adaptation towards existence under conditions of intermittent moisture or conditions of excessive transpiration) occur; the chief of these is without much doubt the development of secondary pigmentation of the cell walls, which acts as a filter for excessive quantities of light of injurious wave-lengths. Since intense light is without exception correlated with increased temperature and thus increased transpiration, some of the mechanical contrivances such as "lobules," closely imbricate leaves, differentiation into cilia that tend to hold water by capillary action, thicker cell walls, papillose leaves, etc., should perhaps be mentioned under "light" since they occur constantly among those species that are found under conditions of intense light.[40]

EDAPHIC FACTORS

The physical structure and consistency of the substratum, its chemical composition, its ability to retain moisture (relative to its structure and consistency) and other edaphic differences act decisively to delimit the hepatic flora. Some of the locally important factors are as follows:

1. *Structure and consistency of the substratum.*—Whether the substratum is of an organic nature (bark, decaying xylem or decayed xylem and leaves i.e., humus) or essentially inorganic (rock, sandy soil or loamy or clayey soil), decidedly influences the nature of the hepatic flora. The distribution, as regards substratum, of the species is discussed in some detail under each individual form, hence does not have to be discussed here.

Certain general effects of the physical nature of the substratum may be mentioned here, however. Exfoliation of bark of certain trees (*Platanus* as well as the evergreens *Tsuga, Pinus,* etc.) prevents colonization by corticolous Hepaticae. Rapid disintegration of some shales and sandstones prevents colonization by other species; many shale ledges are almost denuded of bryophytes because they disintegrate so rapidly that colonization is scarcely possible; similarly, many shale talus slopes are not colonized or only slightly so because of the loose consistency and rapid erosion. Ability to retain moisture is of great importance; entire groups of species (*Metzgerinae* and *Anthocerotales*) that are mostly unable to withstand periodic dessication are limited usually in occurrence to loamy or clayey soils that retain moisture for relatively long periods of time. On the other hand, some species are able to exist in great quantity on more exposed, sandy soil where they are subject to dessication for most of the growing season; among such species are *Cephaloziella rubella, Lophozia bicrenata,* etc.; the extensive distribution of these species under such

40 See Müller (1916) for data on adaptation of Hepaticae to extreme light.

conditions is evidently due, in part, to the fact that competition is relatively limited since most Hepaticae cannot survive under such decidedly xerophytic conditions.

2. *The composition of the substratum.*—Chemical composition of the substratum is of great importance in delimiting the nature of the hepatic flora. The individual effects of the various important elements have not been studied to any degree.[41] We know however, that certain species occur only in areas poor in available nitrogen (*Sphagnum* bogs). Such species are *Microlepidozia setacea, Lophozia marchica, Mylia anomala,* etc. which often exist in symbiosis with fungi that inhabit the terminal portions of the rhizoids, that are able to fix nitrogen and pass it on to the plant.[42] Other species are very decidedly limited to siliceous regions and appear to have a definite affinity for silica.

Local distribution appears to indicate that a number of essentially "calciphilous" species (*Riccardia pinguis, Cololejeuna biddlecomiae,* etc.) are able to exist on non-calcareous sedimentary rocks but are very rare or absent on siliceous rocks. On the other hand, some species abundant on siliceous rocks are unable to exist to any degree on non-calcareous sedimentary rocks, as shales or sandstones. Our local flora consists largely of species of non-calcareous sedimentary rocks and soils derived from such rocks, as well as of "calciphilous" species of calcareous rocks and their overlying soils. This explains the local frequence or abundance of such species as *Riccardia pinguis, Moerkia flotowiana, Preissia commutata, Lophozia badensis, Lophocolea minor,* etc. The rarity of such species as *Jubula pennsylvanica, Microlepidozia sylvatica, Anastrophyllum minuta, A. michauxii, L. gracilis,* etc. appears largely due to their inability locally to tolerate calcareous sedimentary inorganic substrata. The entire absence (except in the limited siliceous region of the Olean conglomerates) of species like *Plectocolea hyalina, Scapania undulata* and *Jungermannia pumilla* again appears to be traceable partly to this factor.[43]

It therefore appears justifiable to set up three groups, depending on the chemical nature of the underlying rocks: species of calcareous rocks, species of sedimentary rocks neither distinctly calcareous nor acidic, and species of siliceous rocks. Species of siliceous rocks may occur on such sedimentary rocks as quartz conglomerate as long as the cementing material is not of calcium carbonate. It is well known that the distribution-pattern of some species is not influenced by pH as much as it is by affinity for certain elements; it is possible that some of the species of siliceous regions occur on quartz or acidic igneous rocks not because they necessarily "prefer" a low pH but because of a more direct dependency on silica. Certainly, if this were not the case,

41 See Stern (1938) and Voth & Hamner (1940) for experimental work and further citations.

42 For a discussion of the colonization of a nitrogen-free medium by *Cephaloziella byssacea* and *Lophozia bicrenata* see Griggs (1935, 1937). These pioneer species appear to exist only on such unfavorable sites. I have, for instance, found *C. rubella* on a burned carbonized log.

43 The rarity of these species locally is probably due more to climatic factors (temperature) since they show a much wider toleration northward.

such species would not be largely absent on non-calcareous sedimentary rocks.

Other species appear to grow equally well on substrata varying widely both physically and chemically. It is but necessary to cite *Scapania nemorosa* which frequently occurs on decaying logs, moist loamy soil, moist humus, distinctly calcareous shales and sandstones or on siliceous quartz-conglomerate. This species is widely distributed outside of our region on siliceous igneous rocks as well as on basaltic rocks. Such ubiquitous species with wide tolerance and large degrees of adaptability are of course among our most abundant, aggressive, hence successful and widespread species.

Our more uncommon species however, often appear very much restricted in occurrence by pH conditions. It is merely necessary to cite an extreme case. At McLean Bogs, Tompkins County, there occurs an open, floating bog with a shallow pond in its center, fed by brooks draining the calcareous surrounding region; its recorded pH in August ranged from 8.4-9.4. Less than one-half mile away occur two smaller, closed bogs where the prevailing pH is 3.7 to 4.4. In the open bog (Mud Pond) the hepatic vegetation is very restricted, only the "calciphile" *Riccardia pinguis* occurred around the edge where it was constantly kept saturated by the marly bog water; a little further from the edge where *Sphagnum* occurred and the pH was somewhat below 7.0, the tolerant *Cephalozia connivens* was present. In the acid bogs however, the decided oxylophytes *Mylia anomala, Cladopodiella fluitans, Cephaloziella elachista, Lophozia marchica,* etc., are consociated.

Although relatively little actual pH data is at hand from this region, there is a considerable literature on the "calciphile" *vs* "calciphobe" nature of many species. Meylan (1924) gives a chart in which the frequency of the species is indicated on acid *vs* alkaline substrata. His data, to some degree at least, do not agree with the observations given under the species treated on the previous pages. This, I believe, is in part due to the fact that decidedly "calciphile" species usually have a pH range of about 6.5 to 6.8 to 8.0 (rarely higher) and also that many of the "calciphile" species occur as often on substrata with the pH slightly below neutral or merely neutral. It is obvious that high availability of calcium may occur under such slightly acid conditions and that the species may be more conditioned, as regards occurrence, by the calcium concentration than by the mere hydrogen-ion concentration. Meylan appears strictly to consider the species occurring under a pH of 7.0 or less as "calciphobes"—a procedure which may not be quite correct. Recent intensive pH measurements (appearing elsewhere) give a range of 6.5-7.5 for most of the species considered decided "calciphiles" in the literature. This supports the belief that under circumneutral conditions, a range slightly below 7.0 is meaningless in determining whether or not a species should be classed as a "calciphile." For instance *Riccardia multifida* and *Moerkia flotowiana* are in the writer's opinion, decided "calciphiles" since their distribution both in New York and Minnesota where they have been intensively studied, is always correlated with bogs underlain by marl and supporting a dense vegetation of *Thuya*. Actual pH readings vary from 6.5 to above 8.0, yet it would seem scarcely correct to consider the populations occurring under a pH of 6.5-6.9 as "calciphobes."

More recently, Apinis and Lacis (1934-1935) have studied the distribution of Hepaticae in relation to pH, and have presented much objective data. Their work, in a little available publication, is briefly reviewed by Müller (1939). Amann (1928) also discusses the "calciphile," "indifferent" or "calciphobe" nature of many species of bryophytes but has relatively little data on Hepaticae. Rubinove and La Rue (1928) give data on the pH of the sites of various bryophytes in Michigan, and Ikenberry (1936) gives experimental data on the growth and distribution of mosses as related to pH.

Although Müller (1938) found a distinct correlation between the occurrence of "calciphile" Hepaticae and trees with bark high in CaO, no such correlation is noted by Brown (1948) who states: "The epiphytes observed have not shown a marked selectivity for host species. . . . It seems evident, therefore, that the epiphytes appear on any species of host that by reason of its environment and physical features can provide the habitat within the limits of which they can survive or succeed." The latter statement seems, to some degree, an oversimplification since in the writer's opinion there is at least a fair correlation between the occurrence of some Hepaticae and a particular host. *Frullania oakesiana,* a species to be searched for in our *Thuya* bogs, occurs almost exclusively in bogs on White Cedar. Similarly, *Lejeunea cavifolia* and *Cololejeunea biddlecomiae* are extremely rare on bark in most of central and western New York (and are not reported from it in the study of Brown), yet occur frequently on the bark of the calciphilous *Thuya* in Bergen Swamp and similar places.

The Forest Types and Associated Hepatic "Layer-Societies": Microdistribution

Since microclimate and microedaphic conditions frequently, if not as a rule, predominantly affect the local nature and composition of the liverwort flora, some generalized description of the vascular arborescent flora, that so frequently and fundamentally conditions both microedaphic and microclimatic conditions, seems essential. In this connection, some of the more diverse and interesting associated "layer-societies" (synusiae or associules) in which Hepaticae play a considerable part may well be mentioned.[44]

It is a truism that frequently there is a profound interrelationship between the nature of the vascular, and especially the arborescent flora, and the nature of the bryophyte flora. This is obviously to be expected since the general climatic and edaphic features of a region must have some limiting effect on the composition of both groups of plants.[45]

Some species as *Lophozia (Isopaches) bicrenata* are largely limited in local occurrence to a single forest type — the Oak-Chestnut-Hickory type or the

44 However desirable, limitations of space totally preclude the inclusion of the mosses in such a treatment.

45 Like some of the more "aggressive" vascular plants, a considerable number of *Scapania nemorosa* and *Lophocolea heterophylla* have a wide tolerance and occur under a relatively great variety of conditions in several forest types. Such ubiquitous forms are naturally among the most common species.

stages immediately preceding it. Others occur only in two or three stages of a particular seral development, such as *Cladopodiella fluitans* and *Lophozia marchica* which occur only in the Sedge-mat and *Chameadaphne* Associes of the hydrarch bog succession.

Such restrictions in occurrence may be due to two factors: (1) the species may be restricted to a limited environment because its edaphic requirements are similar to those of the association or associes it is found in, or (2) the correlation with a particular arborescent community may be due to the production of a suitable microenvironment by the arborescent forms. As an example of the first type, where similar environmental requirements limited the occurrence of both vascular plants and hepatics, one may cite the occurrence together of *Thuya* and the Hepaticae, *Moerkia, Lophozia (Leicolea) rutheana, Riccardia multifida* and *R. pinguis* as well as *Preissia commutata* in the more open, exposed places. The occurrence together of these species is evidently influenced by a direct dependency on moderate-to-high quantities of calcium carbonate. As an example of the second type, where the vascular flora creates the environment for the bryophyte flora, may be cited the local distribution of *Bazzania trilobata* and *Lepidozia reptans* both of which have a rather low toleration for lime. These species locally are largely limited to the Beech-Sugar Maple-Hemlock Climax and its various subclimaxes in which they occur on shaded, moist decaying logs and the resultant humus which is decidedly acid, and relatively free of lime, although the immediately underlying soil may be quite rich in it.

Many similar examples could be cited but in the majority of cases there is not enough data to clearly establish the exact causes for the correlation in occurrence of specific vascular and bryophyte societies. For instance, it cannot be ascertained from field study alone, whether or not *Lophozia (L.) bicrenatus* is largely limited to the xeric, acid, exposed situations (where the Oak-Hickory-Chestnut Association occurs) because of the inability of this species to compete for more favorable niches or because of a much more positive factor that serves to link it with such conditions (i.e., it may "prefer" such situations). Ochsner (1927), Brinkman (1929) and others clearly appreciate the frequency of this correlation and have suggested using bryophytes as indicators of sites.

Although the following discussion will deal largely with relatively undisturbed areas, there is a limited flora that is associated with the activity of man. Along paths near streams where the soil is so compact that it holds water very tenaciously, and where disturbance is so frequent that erect, larger plants cannot succeed, is one of the best places to look for *Riccia crystallina* and *frostii* and *Ricciocarpus natans* and other *Ricciaceae* as well as *Notothylas, Anthoceros* and *Fossombronia wondraczekii*. Such species appear unable to compete with other bryophytes or erect plants but appear to be able to withstand a relatively high degree of "punishment" at the hands of man. Again, *Marchantia polymorpha* is frequent around burnt-over areas and may even occur in cracks in urban sidewalks. The latter species together with *Lunularia cruciata* also occurs frequently in greenhouses. The last-named in fact is to be

classed as a greenhouse weed, at least in North America.[46]

The following, incomplete and simplified analysis of our major forest types and associated ecological niches is based in part on the published works of Gordon (1940), Bray (1930), Jennings (1927, 1939) and Nichols (1913-1916-1935). Such a classification suffers from the necessity for arbitrary divisions.

General Divisions

It has been well established that central and western New York belong to two distinct vegetational areas, generally considered to be dominated by Climax Associations. These are the Oak-Chestnut-Hickory Association (equivalent to the dominance of Oaks, Hickories, Chestnut, etc., or Zone B of Bray, 1930 and Hotchkiss, 1932, Fig. 5) and the Beech-Sugar Maple-Hemlock-Yellow Birch Climax, also variously called the Hemlock-White Pine-Northern Hardwood Climax (equivalent to the Beech, Sugar Maple, Yellow Birch, Hemlock Zone, or Zone C of Bray and Hotchkiss). The general characteristics are discussed in detail by Bray (1930) and by the students listed in the above introductory notes. The first of these zones is generally considered part of the Deciduous Formation or Panclimax (*Quercus-Fagus* Formation of Weaver and Clements, 1938) while the second is variously considered merely an association within the Deciduous Formation (Nichols, 1935, etc.) or a separate Formation (The Lake Forest, or *Pinus-Tsuga* Formation of Weaver and Clements) or as sometimes considered, a broad ecotone region between the true deciduous and true boreal forests.

In addition to these two major types, remnants of a third major type occur as vestiges of the hydrarch Black Spruce-Tamarack-Fir Bog Forest Subclimax (together with the earlier seral phases, the Sedge-mat and the *Chameadaphne heath*). This essentially, is a remnant of the Northern Coniferous Forest Formation or Panclimax though the *Picea glauca-P. rubra-Abies balsamea* Climax no longer succeeds.

These forest types and associated hepatic layer societies may be briefly outlined as follows:[47]

THE NORTHERN CONIFEROUS FOREST FORMATION, OR PANCLIMAX

This type, essentially part of the boreal Canadian or Canadian-Hudsonian Zone of Merriam or of the Subarctic-Subalpine Zone of more modern students, exists as mere remnants in our area — scattered through some of the more extensive poorly drained or undrained regions, both on the low-lying Ontario Plain and the Appalachian Plateau. It is not known to what degree lower prevailing temperature (due in part to high evaporation), is responsible for preventing direct succession of the prevailing deciduous associations. This

46 This species has a "semi-domesticated" distribution throughout much of the rest of the world except in tropical and subtropical regions.

47 In this outline only the fifty or sixty more common (or more significant) Hepaticae are treated. More than half our species occur so rarely that it is unwise to attempt to evaluate their ecological role locally.

formation is nowhere typically developed and occurs only as the subclimax and the earlier developmental stages. One therefore gets the impression that it has in part, been restricted to more limited, less favorable areas.[48]

This formation is locally to be considered a gradually disappearing, in fact, virtually vanished disjunctional formation, a relic of the immediate postglacial period. Two edaphically controlled seral developments occur locally, dominated by the composition of the underlying soil. Normally these find their climax in the typical boreal Spruce-Fir forests. Locally however, a White Pine-Hemlock-Yellow Birch Subclimax generally succeeds, which from the indicated zonation may eventually be followed by the Beech-Sugar Maple-Hemlock Climax. These two seral developments may be charted as follows:

1. *Calciphilous Sere*[49]	2. *Calciphobous Sere*
Open Marl Bog and Secondary Marl Bog	Open Pond
↕	↕
Sphagnum-Sedge Mat	Sphagnum-Sedge Mat
↕	↕
Chameadaphne Heath	Chameadaphne Heath
↕	↕
Arbor-vitae Swamp	Black Spruce-Tamarack Bog Forest
↕	↕
Pine-Hemlock-Yellow Birch Subclimax	

1. *The Calciphilous Sere.*—This occurs widely distributed on the Ontario Plain in several bogs which are underlain by deep beds of marl. Some of these bogs (as Bergen Swamp) are still in process of formation and deposition of marl by various *Chara* spp., "calciphilous mosses" and by precipitation from limy, spring-fed brooks, is still going on. The best developed of such bogs is that northwest of Bergen, Genesee County, from which the following data are largely drawn.

48 This also occurs repeatedly among the Hepaticae that are of "marginal distribution" in our area. They occur here under much restricted circumstances. *Mylia anomala* and *Calypogeia sphagnicola*, for instance, occur widely in the north on peaty banks at the edges of ledges and cliffs whereas locally they are strictly limited to peat bogs. *Scapania mucronata* locally occurs only as a chasmophyte in the crevices of moist sedimentary rocks; further north it is widely distributed, on peaty banks, on thin soil over rocks, on decaying logs, on rocks in shaded swamps, etc. Again, *Lepidozia reptans* and *Blepharostoma trichophyllum* locally are much restricted in occurrence and are found almost without exception, on decayed logs or the resulting humus. In the north they become much more ubiquitous, being found abundantly on moist shaded rocks (where they may be pioneers or may secondarily invade and creep among other bryophytes), soil, logs, extremely acid peat—in other words, under a vast range so far as pH and nature of substratum go. In the case of the Hepaticae, it may be either a case of restriction to the optimal niches, along the peripheral distribution or they may, along the peripheral distribution, be restricted to somewhat less favorable sites.

49 See Muenscher (1946) for a description of this series of stages and the accompanying vascular plants.

a. Open water. No Hepaticae occur here but *Chara* and "calciphilous" mosses occur in shallow water overlying marl.

b. Open Marl Bog Associes. This includes both the Open Marl Bog and Secondary Marl Bog stages of Muenscher (1946) since they are identical so far as Hepaticae are concerned. *Triglochin, Cypripedium candidum, Zygadenus* and *Parnassia caroliniana* are characteristic forms; others are listed by Muenscher. Late in the Open Marl Bog Associes, as a zone surrounding local calciphilous moss-hummocks, there are a number of secondary invaders among the Hepaticae: the extremely characteristic *Lophozia (Leicolea) rutheana, Moerkia, Riccardia pinguis* and *multifida.* These species occur under pH 6.5-7.5 or even higher.

c. Local *Sphagnum Bog* Associes. This associes occurs locally on elevated areas directly over marl. Although the pH is from moderately to decidedly acid (depending on the distance above the marl bed), there is considerable penetration by calcium ions. A few tamaracks and *Chameadaphne calyculata* as well as *Ledum, Drosera, Sarracenia* and *Chiogenes* are characteristic vascular plants. Index Hepaticae are *Microlepidozia setacea, Mylia anomala, Cephaloziella subdentata, Calypogeia sphagnicola* and *Riccardia multifida.*[50]

d. Arbor Vitae Swamp Associes. Locally this associes directly precedes the subclimax; further northward it itself becomes subclimax and may persist into the climax. In its dense shade a large number of species occur, belonging to several distinct associules:

(1) On bark the *Lejeunea-Cololejeunea-Frullania* facies of the *Frullania-Radula-Lejeunea* Associule[51] is widespread. *Lejeunea cavifolia, Cololejeunea biddlecomiae, Frullania asagrayana* and *eboracensis*[51] and *Radula complanata* are index species. The first two are decidedly "calciphilous," and their common occurrence in marl bogs, on bark, may be traced to the high calcium content of such bark.[52]

(2) On marly, moist ground the *Riccardia multifida-Moerkia* Asso-

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50 It is very significant that the less tolerant species, *Cladopodiella fluitans* and *Lophozia marchica* do not occur here. These seem quite unable to compete under conditions with any considerable concentration of calcium ions. The usually associated species *Mylia anomala* is more tolerant however, and occurs under present conditions. *Lophozia marchica* is apparently replaced by the allied *L. grandiretis* and by *L. rutheana.* Similarly, the decidedly "calciphobous" *Pallavicinia leyllii* is replaced by the pronounced "calciphilous," related *Moerkia* as well as to some extent by *Riccardia pinguis.*

51 Further north, and especially further west, *Frullania bolanderi* becomes abundant and characteristic on *Thuya* bark in swamps and wet woods; it has not been found locally, however.

52 Müller, 1938, pp. 103-105, has investigated the occurrence of "calciphilous" species such as *Metzgeria pubescens,* on bark. He found a distinct correlation between the occurrence of such species on bark and a high CaO content in the ash.

ciule[53] persists but is gradually disappearing because of the shading out of the light-loving *Mylia, Cephaloziella subdentata, Calypogeia sphagnicola* and *Lepidozia setacea. Moerkia, Plagiochila asplenioides* and *Chiloscyphus pallescens,* widespread "calciphiles," tolerating non-calcareous conditions, however, *Riccardia pinguis, Calypogeia neesiana* and several *Cephalozia* species *(connivens, pleniceps),* become the dominant Hepaticae, and both *Conocephalum* and *Marchantia* become frequent. With the accumulation of a distinct humus layer, the less extreme marl-tolerating forms appear, among them *Trichocolea tomentella, Geocalyx graveolans, Calypogeia neesiana* var. *Meylanii,* etc.

(3) With the introduction of somewhat acid surface conditions, seedlings of the Pine-Hemlock-Yellow Birch Subclimax make their appearance. With the gradual death of the *Thuya* stands, the decaying logs lying in the older *Thuya* swamps and the bark around their bases, are invaded by the *Bazzania-Blepharostoma-Lepidozia* Associule of decayed tree-buts and logs. These species, able to tolerate only slight amounts of calcium, and usually with a low light tolerance, include *Bl. trichophyllum, L. reptans, (Microlepidozia setacea* occurs as a rarity here), *Odontoschisma denudatum, Jamesoniella autumnalis, Lophozia incisa, L. porphyroleuca* and various *Cephalozia* species (especially *media* and *catenulata*). At this point, the rare *Scapania glaucocephala* also occasionally occurs. The *Riccardia pinguis* rarely persists; it and *R. multifida* are nearly completely replaced by *R. latifrons* (and more rarely *R. palmata*). By the time the succession of these associules is well along, the *Thuya* forest has been nearly completely replaced by the Pine-Hemlock-Yellow Birch Subclimax. This occurs in common with the calciphobous sere and will be treated after the latter.

2. *The Calciphobous Sere.*—This occurs chiefly in the lime-free or lime-poor areas, but may occur in areas (such as the Junius peat bogs) that are calcareous, but where a deep peat layer has completely blanketed the underlying marl. Under the latter conditions (apparently occurring at Plymouth Bog) such bog species as *Scapania paludicola* and *irrigua* may occur as secondary invaders over peat, when conditions have become somewhat acid (by virtue of peat deposition), but when there are still traces of calcium present.[54] Such intermediate stages are locally widespread but for our purposes must be ignored; the following treatment therefore, is of the typical "calciphobous" succession:

53 The term "associule" is used according to Richards (1938) for an aggregation of species, all of one layer, that do not necessarily form a synusia or union but are often merely facies or fragments of synusia. Since the term has certain drawbacks, as proposed by Clements (1936), I tentatively follow the usage of Richards. It would seem better to restrict the term to such societies as the unistratose layer societies on cliff-faces, composed of mosses, hepatics, algae and lichens, that, to all purposes, are climax in nature. If the term is thus restricted, we are faced with using a new one for the facies or stages of synusia (such as on decaying logs) that are in obvious rapid evolution. Though there is a large and unwieldy terminology, there is still none for the cryptogamic layer societies that is entirely satisfactory.

54 At Plymouth Bog for instance, *Cladopodiella* is very rare, indicating perhaps that there is sufficient lime to eliminate such a decided "calciphobous" species.

a. Open Pond. Floating or submerged forms of *Cladopodiella fluitans* have been observed here, but no other forms. *Utricularia cornuta* (and occasionally *vulgaris*) is an index species of this initial stage, and *Lycopodium inundatum* may occur at its edge where the *Sphagnum*-Sedge mat is beginning to succeed. If traces of lime occur, the *Cladopodiella* is usually absent, while *Scapania paludicola* and *Pallavicinia lyellii* may be abundant and may occur as actual aquatic forms (as at Plymouth Bog).

b. *Eriophorum-Rhynchospora* Associes: The Sedge Mat. *Eriophorum virginicum* and *Rhynchospora alba* are characteristic index species; these grow in a matrix of *Sphagnum* with several *Carex* species. The *Vaccinium* species and other Ericaceae do not yet appear (with the exception of *V. oxycoccus*). The peat mosses are carpeted locally by a very distinctive hepatic associule, the *Mylia-Cladopodiella* Associule. *Mylia anomala, Cl. fluitans, Cephaloziella elachista, Lophozia marchica* and *Calypogeia sphagnicola* first become frequent at this stage. These species persist until well after the next associes has succeeded but are gradually replaced by others as the shade becomes relatively dense or when conditions become too mesic because of accumulation of organic matter and lowering of the water table.

c. *Chamaedaphne-Ledum-Andromeda* Associes: The Heath Associes. In the earlier stages the above hepatic associule persists but gradually the more shade-tolerating or "shade-loving" forms as *Pallavicinia lyelli, Cephalozia pleniceps* and *C. connivens* succeed, with a gradual disappearance of the *Mylia-Cladopodiella* Associule.

d. *Picea-Larix* Associes: The Black Spruce-Tamarack Forest Associes. Further north this is subclimax or (in the far north) even climax over large low-lying areas. Locally it is merely a strongly compressed zone, superseded soon by the Pine-Hemlock Subclimax or faciations of this subclimax. At the point in development when the tamarack and spruce appear, *Cladopodiella, Mylia* and *Calypogeia sphagnicola* gradually disappear except in isolated openings.[55] *Pallavicinia, Cephaloziella elachista,* the several *Cephalozia* spp. *(pleniceps, macrostachya, connivens)* and *Lophozia marchica* persist well towards the end of this stage. On rotting logs in this associes an entirely new group of species (*Lophozia incisa, L. porphyroleuca, Odontoschisma denudatum, Jamesoniella autumnalis, Riccardia latifrons, R. palmata, Jungermannia lanceolata,* etc.) make their appearance. These invading species however, are more characteristic of the next stage.

Locally this associes is succeeded by the following two stages of the Hemlock-Hardwood Formation:

e. The Pine-Hemlock-Yellow Birch Subclimax. This rather extensive zone, very variable in characteristics, with often some black ash, balsam fir, red maple, mountain ash and American elm, is quite variable in degree of

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55 Further northward however, these species persist until long after the Spruce-Tamarack Forest succeeds. They then become limited to the margins of paths cut through the open forest by deer, on the vertical, wet sides of which they occur.

development. Its general characteristics are the same as for the White Pine-American Elm Swamp Forest, listed by Gordon (1940). The Hepaticae occurring here are the same as for the Spruce-Tamarack Forest Zone, with the complete disappearance before this stage is reached, of all the members of the *Mylia* Associule. *Lophocolea heterophylla, Plagiochila asplenioides, Bazzania trilobata, Calypogeia neesiana* var. *meylanii* and *trichomanis* (swamp forms), *Cephalozia catenulata, Harpanthus scutatus* and *Trichocolea* become common in the swamp forest together with the above species. The nearly universally found *Nowellia curvifolia* and *Lophocolea heterophylla* are very abundant and persist into the climax together with the limited quantities of *Plagiochila asplenioides* and *Calypogeia trichomanis*. *Ptilidium pulcherrimum* is not too common in this subclimax but becomes more frequent as conditions become more mesic; under present conditions, it and *Bazzania trilobata* occasionally are able to invade bark. On the latter substrate, *Radula complanata* is a characteristic species together with *Frullania asagrayana* and *Porella platyphylloidea*. These corticolous species virtually disappear as the denser shade and less humid conditions of the climax are approached, but *Frullania eboracensis* persists in more open regions. The favorable water balance (humidity plus rainfall/evaporation) results in nearly as rich a development in this stage, of corticolous forms, as in the early stages of the Mixed Mesophytic and Beech-Maple-Hemlock Climaxes of the ravine slopes or bottoms. This type of subclimax is common throughout much of the low-lying, poorly drained areas (Michigan Hollow Swamp, Freeville Swamp, Slaterville Swamp, etc.) where virtually no trace is left of the earlier coniferous formation (except for isolated, often large and old trees of fir and tamarack).

f. The Beech-Sugar Maple-Hemlock Climax. The zonation about some bogs indicates that this climax community may eventually succeed. *Betula lutea* and *Acer rubrum* are frequent accessory species, both persistent from the subclimax as is hemlock and to a lesser degree, white pine. The exceedingly dense shade eliminates a number of species; of more importance is the dense litter and layer of dead deciduous leaves which make the forest floor a highly unsuitable place for development of a well-developed bryophyte flora. A few species (*Lophocolea heterophylla, Ptilidium pulcherrimum,* etc.) as noted above persist, largely on decaying logs. Under typical conditions, the corticolous species are virtually or quite shaded out as the climax is attained.

THE DECIDUOUS PANCLIMAX
THE BEECH-SUGAR MAPLE-HEMLOCK-YELLOW BIRCH AND THE OAK-CHESTNUT-HICKORY CLIMAXES

In its varied, complex and frequently strongly interdigitated manifestations, this formation covers virtually all of the region discussed, except for the traces of the Northern Coniferous Formation briefly treated above. In addition to the obvious complexity due to postglacial migration, the extensive disturbance by man during the last two hundred years has manifestly altered the entire nature of this panclimax. Much of the land at one time covered by primeval climax forest is today in a more or less perpetual subclimactic state.

In addition to the Beech-Maple-Hemlock-Yellow Birch Climax, which appears to be the climatic climax throughout all or nearly all of the region here treated, there are large areas of Oak-Hickory (at one time largely Oak-Chestnut-Hickory) which occupy varying positions in succession. On the south-facing ravine crests they may be largely edaphic climaxes while on the sunny crests of some of the high hills (South Hill, near Ithaca) they may possibly be of the nature of climatic climaxes. In addition, the valleys harbor traces (perhaps advance-guards, perhaps relics of an xerothermic period) of the Appalachian Mixed Mesophytic Forest. Such species as *Magnolia acuminata, Nyssa sylvatica, Liriodendron tulipifera, Carya cordiformis* as well as the locally more widely distributed *Betula lenta, Quercus borealis, Fagus grandifolia, Quercus montana, Castanea dentata, Prunus serotina, Tilia americana,* etc., locally result in areas that have many of the characteristics of the Mixed Mesophytic Forest. Furthermore, on many of the hills and richer slopes, the climax forest becomes quite different in nature from that occurring over the area as a whole: hemlock and yellow birch virtually disappear and a true Beech-Maple Climax apparently results, frequently with the development of a Beech consociation.

Since the latter associations are relatively infrequent and since major features of the forest floor approach those obtaining in the Beech-Maple-Hemlock-Yellow Birch Climax only the successions in the latter climax are treated here. It is to be understood therefore, that where the Beech-Maple-Hemlock-Yellow Birch Climax is mixed with or replaced by Mixed Mesophytic Hardwoods, or attains the more restricted Beech-Maple phase, the hepatic population is usually largely the same except for such exceptions as are noted below.

The Oak-(Chestnut)-Hickory Climax (edaphic or climatic as the case may be) however, is so very different in nature, as well as in the successions leading to it, that it is treated in rather full detail below.[56] The distribution of our two major deciduous forest types is of some significance. The Beech-Maple-Hemlock-Yellow Birch Climax occurs over most of the Appalachian Plateau area and locally acquires a very northern aspect (as in swamps and bogs) because of the scattered islands of the Northern Coniferous Formation contained within it. Southward (i.e., at higher elevations) this forest is nearly continuous except for dissection by valleys in which the Oak-Hickory (or occasionally traces of the Mixed Mesophytic Hardwoods) type occurs. Northward and westward, as the Ontario-Erie Plain is approached, the Beech-Maple-Hemlock-Yellow Birch Forest becomes limited to the north-facing slopes of the isolated higher plateaus and hills while broad valleys and south-facing slopes are mostly covered by the Oak-Chestnut-Hickory Climax. On the Ontario Plain, except in bogs and swamps, hemlock and yellow birch become relatively infrequent and a combination of Oak-Chestnut-Hickory Forests as well as various deciduous swamp forests (rich in silver maple, red

56 The region covered here, by the definition of some workers, has Oak-Hickory Forests that are only subclimactic while similar forests not far to our south, below the glacial boundary, are of climax nature. Obviously the Oak-Hickory forests in this more or less intermediate area, often cannot be clearly considered either climax or subclimax. The assignation to one or the other is therefore a purely academic point.

maple, etc.) obtain. However, in the larger bogs on the Ontario Plain there recur traces of the Beech-Maple-Hemlock-Yellow Birch Climax. Indeed, the bog depressions result in vegetation similar to that expected on sudden high elevations: in the center, traces of the Northern Coniferous Climax occur (usually the "calciphile" *Thuya-Tamarack* Associes), surrounded by a White Pine-Hemlock-Yellow Birch Subclimax, followed by the Beech-Maple-Hemlock-Yellow Birch Subclimax, which in turn is followed by the Beech-Maple-Hemlock-Yellow Birch Climax.[57] Local distribution therefore indicates that the Oak-Chestnut-Hickory Forest (and allied Mixed Mesophytic Forest) is decidedly of southern affinity. The virtual absence of any trace of "northern" Hepaticae within it together with the development (or survival) of a significant northern hepatic element in the climax occurring over the Plateau region, supports such a view. This apparently fundamental difference has been emphasized by Weaver and Clements, 1938.[58]

This division of the region into two general zones, one of northern affinity and one of southern affinity, has been long recognized. The northerly affined forest of the plateau region is that of Zone C of Bray (1930), or Zone of Dominance of sugar maple, beech, white pine, hemlock, yellow birch mixed forest. This essentially falls into the Alleghany-Transition Zone of Merriam.

The southerly allied region is the Zone B of Bray (1930) or Zone of Dominance of oaks, hickories, chestnut, etc. Gordon (1940) divides this into two fundamental regions. He reserves the term Mixed Mesophytic Forest for the zones occurring up the river valleys of the Appalachian Plateau while he uses the term Beech Forests and Deciduous Swamp Forests for the region on the Ontario Plain.[59] Jennings (1927, 1939) has also treated these associations and their succession but has given what appear to be faciations and lociations of one associes, associational standing. His analysis into a multitude of associations is not strictly applicable since many of the forest types treated by him are so interdigitated and telescoped locally, that any attempt at differentiation is pointless for our purposes.

With this introduction some of the more significant successions in which Hepaticae play a part or occur in significant quantity, may be treated. It should be kept in mind that neither the very xeric nor hydric initial stages, nor (especially) the mesic, uniform, climatic climax are ever very rich in Hepaticae. In the former case, there has usually been either not sufficient time for invasion or ecesis, or insufficient preparation by lichens or pioneer mosses, to make development of much of a hepatic flora possible, even if ecesis could occur. In the latter case, the dense shade together with the extreme uniformity of conditions plus the annual accumulation of a deep litter of dead leaves (which would tend to cover and bury any ground cover), virtually eliminate all but a very few hardy, persistent and extremely tolerant species. The most abundant development of Hepaticae, both as regards

57 Frequently the climax is scarcely evident surrounding such boggy regions and its succession is presumptive, at best.

58 They consider the Beech-Maple-Hemlock-Yellow Birch Climax as part of the "Lake Forest," a formation distinct from the Deciduous Formation.

59 Both would fall into the "Carolinian" of Merriam.

number of species and individuals, occurs in the intermediate stages in which there is the greatest diversity of terrain and the greatest differentiation into ecological niches. It is therefore in the seral stages, from shortly after the initial stage until the subclimax is reached, that Hepaticae play the most important part in deciduous forests.[60]

Certainly, the uniformity of substrate, light and moisture as well as the unfavorable effects of the accumulation of litter, occurring in the climax, eliminate most species of Hepaticae and other bryophytes. Furthermore, the climax communities persist locally only as much disturbed remnants from which the more sensitive, less tolerant species of Hepaticae have long since vanished. The original hepatic flora of the climax locally is thus a matter of conjecture and it is certain that it was never very rich except in initial or subinitial areas (as exposed loam banks, lying within the climax but prevented from attaining a climax nature by slope, exposure, etc.).

Since insufficient data are at hand to clearly establish successions, either of the arborescent flora that conditions the bryophytic ground layer, or of the bryophytic flora itself, a more static treatment follows than is desirable. Because of the numerous actual successions together with their variations and the large number of true climaxes, no other course seems possible at present — the complexity of the subject is too immense. On moist vertical rock faces, for instance, there may be several successions which have resulted in several different climax communities — the kind dependant on the factors of exposure, water-supply and edaphic conditions. To all intents and purposes, each of these communities which may undergo several stages, ends in a bryophytic society, that with existing climatic features and without topographic degradation, is of absolutely climax nature.

As an example may be cited the sere existing on north-facing, calcareous ravine walls where there is some seepage and where the humidity is usually quite high. Here the initial stages are formed by bacterial colonies, various small algae (diatoms, blue-green algae such as *Nostoc, Anabaena, Tolypothrix*) and occasionally such green algae as *Trentepholia.* These serve as a matrix in which the ecesis of spores of such mosses as *Gymnostomum* may take place. The *Gymnostomum* essentially forms a climax community on such cliffs, often with the invasion of secondary species such as *Lophozia badensis,*[61] *Preissia* or *Pellia fabbroniana.* When this stage is reached, the

60 This is less striking in the case of the Coniferous Formation where the Hepaticae play a part, though subsidiary to that of the mosses, even in the climax forest. This difference as regards representation in the climax and subclimaxes is largely attributable to the difference in nature of the quantity and quality of forest litter: the needles of the coniferous forest produced in relatively small quantity and dropped gradually over a long period of time, do not result in as dense a litter nor do the coniferous forests produce as dense shade as do the trees of the deciduous climax.

61 *L. badensis* may undergo ecesis on such algal films directly without previous preparation by *Gymnostomum* or other small mosses, as I observed both at Fall Creek and Sixmile Creek. The species, then is considered as a "pioneer." Strictly, it is of course not a pioneer since it apparently must have some preparation of the rock surface and therefore cannot undergo ecesis on absolutely bare rock walls. However, the previous colonization by bacteria and various small algae has been very generally ignored in the past.

actual weight of the saturated moss-mat together with freezing and ice-action seem to keep such a community from advancing further unless the cliff-wall is fissured and offers opportunity for ecesis of small vascular plants (*Primula mistassinica, Pinguicula vulgaris, Arabis lyrata, etc.,* or ferns). It would seem that the colonization by small vascular herbs on such rock-walls is very sporadic and always dependent on the presence of crevices, offering a more secure anchorage. On vertical unfissured rock-walls the bryophyte societies are absolutely climax. Occasionally after gradual growth and thickening of the moss-mat, sudden drenching by rain may result in such a sudden increase in weight that the climax community is torn loose and destroyed. However, this is followed by reestablishment of the original community.[62]

THE XERARCH OAK-HICKORY COMMUNITY, AND ASSOCIATED COMMUNITIES

Jennings (1939) recognizes seven "successional" stages here, the first six "Associations" (Pitch Pine, Chestnut Oak, Chestnut, Scarlet Oak-Black Oak, White Oak, Red Oak-Basswood-White Ash) culminating in the Beech-Sugar Maple Climax.[63] Locally the marginal stages are much telescoped, with the Pitch Pine Community very local in occurrence, and often not even developed in which case the Oak stage is the "initial" stage. The other "preclimactic" stages are so interdigitated and compressed, in most areas, and the associated hepatic communities so simple, that the following simplified treatment suffices:

1. *Pitch Pine Community.*—This represents a very xeric stage, occurring frequently on the strongly insolated south-facing[64] crests of the wider ravines[65] as well as on some of the better drained, drier knobs of the hills. It is not nearly as well developed here as further south and is a very narrow, compressed "zone" margined by the oak and oak-hickory zone (at A′ in Fig. 12). The vascular flora is constituted largely by pitch pine, occasionally supplemented (on less extremely dry crests and knobs) by red pine *(P. resinosa)* which may virtually replace it, and the shrubby species, low blueberry *(Vaccinium pennsylvanicum),* New Jersey tea *(Ceanothus americana)* and Moss pink *(Phlox subulata).* On very dry, rocky crests and slopes red cedar *(Juniperus communis),* bear berry *(Arctostaphylos uva-ursi)* and occasionally or rarely *Selaginella rupestris,* largely replace the above forms.

The invading Hepaticae are very few and extremely xeromorphic, with

62 Critical study of ecesis and succession on such sites would be extremely valuable. It would teach us much regarding the actual processes of succession that today are presumptive and too subjectively delineated.

63 The successions assumed by Jennings involve degradation or other forms of topographical change, hence are not successional in the strictest sense. For that reason, I use the term *community* on the following pages rather than *associes,* so as not to imply a succession that would not occur, except following physiographic modification. In other words, the Pitch Pine Community under existing topographical and climatic conditions is climax where it occurs on the ravine edges or hill-tops and is not an initial stage in forest succession.

64 Rarely occurring on exposed, sunny north-facing crests, as at Coy Glen.

65 At A′ to B′, in Figure 12.

thick-walled cells, erect leaves and usually strong pigmentation. *Lophozia bicrenata* and *Cephaloziella rubella* are the common invading species here as in other exposed, xeric, well-drained areas, very occasionally accompanied by poorly developed *Ptilidium pulcherrimum* and rarely by *Lophozia barbata*. Corticolous species are virtually absent.

2. *Chestnut Oak and Oak-Hickory Community.*—This, depending on local conditions, is a very diversely developed zone. The less xeric *Pinus resinosa* persists throughout much of the early stages of this subclimax and is accompanied by a variety of oaks *(Quercus montana, coccinea, velutina, borealis* var. *maxima),* hickories *(Carya cordiformish, glabra* and *ovalis)* and formerly by chestnut (*Castanea dentata*). Jennings (1939) treats the various stages of this stage, which is often little distinct from the subclimax in detail.

The understory is formed by *Amelanchier sanguinea, amabilis, humilis, canadensis* and various *Ericaceae (Vaccinium stamineum, pennsylvanicum, Gaylussacia baccata, Rhododendron nudiflorum,* etc.*)* while such herbaceous species as *Desmodium* spp., *Lupinus perennis, Lespedeza* spp., *Commandra umbellata* and *Houstonia coerulea* form a predominant element, together with the species from the initial, pitch pine stage.

The same Hepaticae persist and become more common. Under slightly moister conditions *Jamesoniella autumnalis* invades.[66] When the forest becomes relatively densely developed, the first corticolous species appear: *Frullania eboracensis,* much more rarely *F. brittoniae.*[67]

Under somewhat mesic conditions, especially in ravines, the open loamy slopes often support several other species besides the usual *Lophozia bicrenata-Cephaloziella* Associule. *Plectocolea crenulata* and rarely *Lophozia barbata* appear under more mesic conditions yet, accompanied by individual plants or small patches of *Fossombronia wondraczekii.* These species represent a semi-xeric phase of the loam bank *Blasia-Pellia-Anthoceros-Notothylas* Associule. Such an aggregation of species is generally accompanied by such vascular plants as *Melampyrum lineare, Gaultheria repens* and *Epigea repens.*

It is evident from the above that the species occurring are usually very few and comprise only an infinitesimal and unimportant place in the successional picture. The invasion by the *Lophozia bicrenata-Cephaloziella* society together with xeric mosses and *Cladoniae* however, often serves as a necessary preliminary to the ecesis of the smaller vascular species enumerated above.

With the development of denser shade and accumulation of more forest

66 In a few places, as on South Hill near Ithaca, there occur acid swampy, sunny areas where the *Ericaceae* are abundant and are accompanied by various species of *Carex, Linum virginianum, Hypoxis hirsuta* and *Habenaria lacera.* Here occur *Lophozia mildeana* and *Scapania irrigua* under relatively moist conditions while *Plectocolea crenulata* and the usual *Lophozia bicrenata-Cephaloziella* Associule occurs under more xeric conditions. This acid swamp succession, resulting in Oak-Hickory Edaphic Climax normally, is very local in occurrence here, and so unimportant that it is not mentioned further.

67 These represent the first members of the "xerophile" *Frullania-Radula-Lejeunea* Associule to invade.

litter, all of the above species gradually drop out and are replaced by other species.[68]

THE HEMLOCK RAVINE COMMUNITIES

Several somewhat subjectively conceived "successional" stages recognized here by Jennings (1939) will be omitted here. The succession presumed by Jennings represents, according to some workers' concepts, a zonation with the nature of the forest types controlled by the slope, thickness and nature of soil and other factors that are largely controlled by the degree of topographic degradation that has occurred. Since similar microenvironments occur throughout many of the societies listed by Jennings, they are treated here as a unit since many of the cryptogamic associules are the same, despite the composition of the ravine forest.

The occurrence of the Hemlock Ravine Communities is mapped in Fig. 12. It is to be noted that in idealized east-west running ravines (Taughannock, Fall Creek, etc.) the Mesarch successions and the Hemlock Ravine Communities occur only on the north-facing sides.[69] In such ravines, the Hemlock-Yellow Birch-White Pine Forest which appears to be subclimax essentially but locally remains as edaphic climax because of topographic features, occurs. In the narrower ravines it occurs at *A* and *B* while in the broader ravines with better developed and greater talus slopes, it forms a dense forest at *D*. In the widest ravines the climax Maple-Beech-Hemlock Forest may eventually develop on such broad talus slopes, though Hemlock usually remains in a dominant position. At *E*, if there is much of a stream-bed, there may be local colonies of the Maple-Beech-Hemlock Climax forest but in many ravines there are traces of the Mixed Mesophytic Forest here.

As has been stressed above, in the wider ravines with strong insolation of the south-facing talus, cliff-walls and cliff-crests, there is little or nothing developed from *D'* to *C'* except occasionally a very xerarch Red Cedar Community (as at Taughannock) with development of the Pitch Pine (or locally Red Pine-Pitch Pine) communities where degradation has proceeded further, and where a more gentle and complete talus slope exists. The south-facing crests (at *B'*) harbor the Pitch Pine Community while directly behind it (*A'*) exist various forms of the Oak-Hickory Chestnut Forest. The Hepaticae of these have been treated above.

68 Whether this stage is climax (as it appears to be on many ravine crests) or subclimax, the hepatic flora is the same, and equally restricted. Whether zonation indicates eventual succession by a Beech-Maple-Hemlock Climax, those species characteristic of it (see beyond) gradually come in and the xerarch *Lophozia bicrenata-Cephaloziella* Associule disappears.

69 This occurs in the wider ravines. In the narrow deep ravines there is little differentiation between the southern and northern walls because the dense forest at *A* and *B* intercepts much of the sun, with the result that the south-facing ravine walls (and talus slopes) (below x, Fig. 12) have little more insolation than the north-facing walls, hence the same forest type develops there and identical hepatic associules occur. This is the case, for instance, to a large degree in all or parts of the ravines of Coy Glen, Lick Brook, Buttermilk Glen and parts of Enfield Glen. Often depending on local conditions, the south-facing slopes have both types alternating.

In contrast to the xeric, bryophyte-poor, south-facing ravine walls, the north-facing ones are extremely rich in bryophytes. These zones may be briefly outlined as follows:

A. The Hemlock-Yellow Birch Ravine Crest Forest.—On the north-facing slopes and often the nearly flat area lying behind it, there is a subclimax of yellow birch and hemlock, often with development of the climax, in part or entirely. The Hepaticae are usually relatively limited in species and numbers.

B. Near or at the crest of the ravine (at *B*) more exposed conditions prevail. Here occurs an associule of epipetric and chasmophytic species, formed by *Lophozia ventricosa,* occasionally *excisa, Scapania nemorosa Diplophyllum apiculatum,* occasionally *Tritomaria exsectiformis* as well as *Bazzania trilobata, Jamesoniella* and *Lophozia incisa* on the thicker, peatier layers of soil that cap the crests. This is a variant of the *Lophozia-Scapania* Epipetric Associule. It occurs chiefly under small hemlocks that are found in the crevices of the cliffs.

C. On the vertical cliff-walls (which may be more or less broken by horizontal shelves, on which may accumulate talus, with approximation to conditions as at *B*), occur a number of associules, all primary societies that do not evolve beyond the herb stage; these are all essentially faciations of the wide-spread mesic *Lophozia-Scapania* Epipetric Associule (on moist rock-walls) or of the xeric *Frullania-Radula-Lejeunea* Associule (on dry rock-walls).

1. *The Lophozia-Scapania Associule.*—This exists in several facies (as follows) but is usually associated with creviced and fissured rock-walls where there is more retention of moisture in soil-filled crevices, hence more mesic species can survive.

a. The "calciphile"*Lophozia badensis* facies: On calcareous sandstone (or shale) rock-walls where there is relatively dense shade, *L. badensis* invades (often among mats of *Gymnostomum*) together with *Pellia fabbroniana* and occasionally *Scapania mucronata* and *Preissia quadrata.* These species however, are mostly chasmophytic and are typical also of the talus zone (*D*). Where there is some soil accumulation or in crevices, *Reboulia* and *Mannia rupestris* occasionally occur.

b. The "calciphobe" *Lophozia ventricosa* facies: On rock-walls of non-calcareous shales and sandstones, often in more exposed areas, *L. ventricosa* occurs together with such species as *Tritomaria exsectiformis* and *exsecta,* occasionally *Scapania nemorosa,* etc. Further north and to some degree in the cold, high situations in Cattaraugus County, similar societies much richer in species, occur in analogous situations or on the north-facing sides of large boulders and ledges lying in forests. Here then occur in addition *Bazzania denudata, B. tricrenata, L. (Orthocaulis) attenuatus, Lophozia longidens,* etc.

2. *The Frullania-Radula-Lejeunea Associule.*—This consists of a number of facies, all of which agree in being composed of more strictly primary species (invading often on virtually bare dry rock walls, or after little preparation by

lichens) which are able to survive under the extremely intermittent moisture conditions prevailing on rock walls. Depending on the degree of exposure and the associated moisture conditions, several faciations are to be distinguished, listed in increasing degree of xeric conditions tolerated:[70]

a. The *Metzgeria-Radula tenax-R. obconica* Facies: On rather shaded vertical rock-walls, in their crevices and on narrow ledges of such rock-walls under conditions of only occasionally intermittent moisture, occur *M. conjugata* and the two more mesic species of *Radula, (obconica* and *tenax).* The latter species, in fact, is so nearly mesophytic that it usually occurs in a nearly pure form (Sixhundred Ravine) while in nearby, slightly more exposed sites, the *Metzgeria* and *Radula obconica* occur together or in pure mats. Although one would expect this facies to grade into the above, it does not do so because of the fact that it occurs more strictly on bare rock faces with little or no development of a soil layer. In areas of higher rainfall this associule may occur on the bark of trees as in the rain-forests of the Smoky Mountains.

b. The *Radula complanata-Porella-Frullania* Facies: On drier, often totally unfissured rock faces, this primary society is very widespread. The *Radula* is accompanied on the less extremely xeric rock walls by *Lejeunea cavifolia* and *Cololejeunea biddlecomiae* forming what amounts to a virtually distinct facies. On more xeric rock-faces it is accompanied by *Porella platyphylla* and *Frullania asagrayana* (rarely *eboracensis*), forming the extreme xeric phase or facies. Both of these societies occur on both calcareous as well as non-calcareous rocks, without too much difference, except for the fact that the *Radula* and the *Cololejeunea* (and to a lesser degree the *Lejeunea*) tend to drop out under non-calcareous conditions. Both societies occur also on bark locally (unlike the more mesophytic *Metzgeria-Radula tenax-R. obconica* Facies) though such corticolous phases are restricted in this region of moderate rainfall to the ravines and swamps where the humidity is obviously higher.

3. *The Reboulia Associule.*—On moderately dry, shaded or somewhat exposed rock-walls, often associated with crevices but not invariably so, *Reboulia hemisphaerica* forms a distinct facies, usually occurring by itself under conditions drier and with moisture more intermittent than in the phases of the *Lophozia-Scapania* Associule in which *Preissia* occurs. Although frequently occurring under conditions nearly as xeric as does the *Metzgeria-Radula obconica* phase of the *Frullania-Radula-Lejeunea* Associule, the *Reboulia* usually occurs by itself, largely because of the fact that it appears to require a certain amount of soil while such a thin soil layer is not tolerated by the *Frullania-Radula-Lejeunea* Associule.

D. The north-facing talus slopes (at *D,* Fig. 12) are very variable, consisting of either forested slopes (with dense hemlock-yellow birch stands, sometimes with much *Quercus montana* admixed and with a shrub layer consisting of *Acer pennsylvanica* and *spicatum* and *Taxus,* or with only a herb-shrub

70 Corticolous bryophyte communities have been studied in detail by Billings and Drew (1938), Cain and Sharp (1938), Olson (1917) and others. The latter worker has also studied succession on bark in some detail.

layer (*Parnassia caroliniana, Geranium robertianum, Pinguicula* and *Primulla* occasionally, etc.). The first represents a later stage, occurring on extensive talus slopes; the latter an earlier stage, occurring on narrow or young talus slopes, or on largely drier talus slopes as at Taughannock. On these talus slopes there is no trace of the more primary *Frullania-Radula-Lejeunea* Associule (except very rarely as at Briggs Gully where *Frullania asagrayana* and *Lejeunea cavifolia* were occasional on the exposed talus) but various faciations of the *Lophozia-Scapania* Associule are very common:[71]

1. Immature talus slopes without an arborescent cover.

1. The mesic "calciphile" *Lophozia badensis* facies: Occurring much as noted for the rock walls but with *Scapania mucronata* more common as a chasmophyte pioneer and with *Conocephalum, Preissia, Marchantia,* occasionally *Mannia rupestris* and *Pellia fabbroniana* occurring.

2. The mesic "calciphobe" *L. ventricosa* facies: Occurring in nearly identical form as noted for the rock wall zone, and usually much better developed than on the vertical rock walls and richer in species. In addition, there may be a somewhat xerarch phase of this facies in which *Lophozia bicrenata* and *L. barbata* as well as *Lophocolea minor* occur. This latter phase occurs chiefly on mature talus slopes and grades into the loam-bank associules.

3. The mesic-hygric "calciphobe" *Gymnocolea-Cephalozia bicuspidata* facies: Occurring only at the foot of sepage moistened and rather sunny, acid talus slopes. The only such slopes known to me in this region are at Taughannock and at Briggs Gully. The facies is best developed at Taughannock where *Cephaloziella byssacea* and the var. *scabra* are associated with it, as well as *Calypogeia neesiana* var. *meylanii*; at Briggs Gully these species are also present but there is no trace of the *Gymnocolea*. This relatively northern society, because of the virtual absence of the required combination of conditions (intense insolation, seepage, and acid pH), is very rare in our area. The occurrence with *Cephaloziella byssacea* is very constant in my experience, elsewhere as well as locally.

2. Mature talus slopes with an arborescent cover.

On such forested talus slopes the subclimax nature of the forest, with availability of an entirely new series of sites, including a larger organic increment (bark, decaying logs, humus, etc.) results in the appearance of a large number of species that did not occur previously. There is therefore a correlated series of successions of the bryophytic communities (associules), from the communities of the immature talus slopes (with their relatively higher insolation and largely mineral nature of the substrata) to the communities of the mature talus layer. The *Lophozia badensis* and *L. ventricosa* facies of the *Lophozia-Scapania* Associule persist on talus slopes until small hemlocks and yellow birches (up to 16-20 feet high) have gained a foothold. The

71 In fact, in many ravines, as at Lick Brook, there is very little difference between the crest and the talus slopes.

Gymnocolea-Cephalozia bicuspidata facies, because of its lack of toleration for shade, disappears much earlier however. With the succession of a subclimax Hemlock-Yellow Birch Forest, the following communities may be expected (in addition to relics of the more initial *Lophozia-Scapania* Associule):[72]

a. Societies occurring largely or entirely on organic matter.

1. *Frullania-Radula-Lejeunea Associule of exposed, xeric bark.*—*R. complanata, Frullania, eboracensis* and *brittoniae*, etc., and *Porella platyphylloidea*, very exceptionally *Lejeunea cavifolia* and *Cololejeunea biddlecomiae* are the characteristic species. The latter two are intermediate in their humidity preferenda to the following Associule.

2. *Microlejeunea-Metzgeria Associule on shaded, sheltered bark.*—*M. ulicina* and *Metzgeria furcata* forma *ulvula* are diagnostic species here, forming a distinct associule in the deepest, coldest, most humid ravines where the atmospheric moisture is at all times very high. *Cololejeunea, Lejeunea* and *Radula complanata* are frequently found under similar conditions but these species are also able to stand conditions of greater insolation and lower humidity. Exceptionally (Lick Brook) *Anastrophyllum hellerianus* occurs under such conditions on bark.

3. *Nowellia-Jamesoniella Associule of decaying, decorticated logs.*—This exists under several distinct facies, a more exposed and xeric, and a shaded, mesic form (see Fig. 13) as follows:

a. Nowellia-Jamesoniella-Ptilidium facies: Occurring on relatively sunny, dry, xeric logs. *Nowellia curvifolia, J. autumnalis* and *P. pulcherrimum* are the index species, often accompanied by the more ubiquitous *Lophocolea heterophylla* and occasionally by *Odontoschisma denudatum.*

b. Cephalozia-Riccardia facies: Occurring on moist, sheltered logs. *Cephalozia media* and *catenulata* (occasionally other species) are here accompanied by *Riccardia latifrons, Harpanthus scutatus, Chiloscyphus, Scapania glaucocephala, Anastrophyllum hellerianus, Blepharostoma trichophyllum, Lepidozia reptans, Jungermannia lanceolata* and occasionally by *Scapania nemorosa* and *mucronata, Lophozia incisa* and *porphyroleuca.*[73]

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72 The extraordinary diversity in niches, ranging from various initial stages on outcrops of persisting bare rock to the stages of humus-banks on deeply forested slopes, contributes to the wealth of species and often dense populations of bryophytes that occur in the ravine regions. The extreme variations in edaphic conditions as well as climatic conditions (determined largely by degree of exposure and amount of available moisture) further contribute to the profusion of niches. This great variation in the nature of the habitats available, often within a few feet, results in the development of numerous societies, most of which obviously intergrade at points of intergrading substratal and climatic conditions. The following scheme is, of necessity, greatly simplified and includes only the more distinct and striking of the societies in which Hepaticae play a part.

73 This facies often may be almost a pure *Lepidozia-Blepharostoma* community, especially on logs in a more advanced stage of decay, on which *Bazzania trilobata* has undergone ecesis. Here there is obviously succession to the next associule.

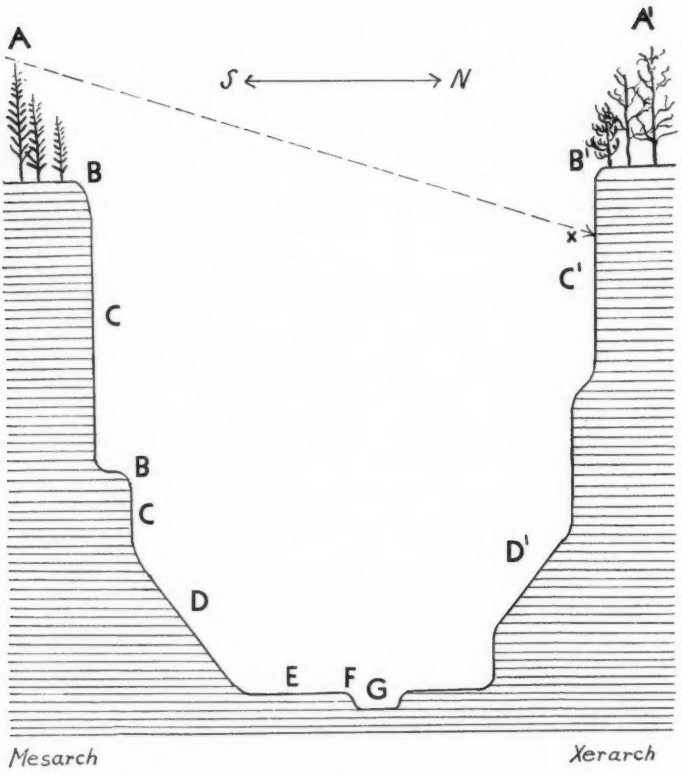

Fig. 12.—Idealized cross-section of an east-west running ravine.*

4. *Bazzania-Blepharostoma-Lepidozia Associule.*—Occurring on moist, shaded humus and much disintegrated wood, forming a humus-bank community. *B. trilobata* and *L. reptans* are accompanied by *Plagiochila asplenioides, Blepharostoma trichophyllum, Geocalyx graveolans, Jungermannia lanceolata* and occasionally *Jamesoniella, Calypogeia, Lophocolea heterophylla,* etc.

Associules 1-4 stand in direct successional relation to each other (see Fig. 12). This is one of the few obviously distinct successions that can be treated without much subjectivity.

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* The letters correspond to the section-headings on pages 662, 663, 668, 669.

b. Societies occurring largely or entirely on mineral matter.

1. Occurring on friable, loose, inorganic matter.

1. *Trichocolea-Moerkia-Riccardia Associule.*—Occurring on more or less calcareous, swampy or springy slopes. *T. tomentella, M. flotowiana* and *R. pinguis* are the index species; frequently with *Lophocolea heterophylla* (ubiquitous) as well as with *Conocephalum* and *Marchantia* present. Very often in our region, the small *Equisetum variegatum* is associated with this associule. Variants of it occur along marly ditches (Bergen Swamp) and in subclimax stages of marl-bogs (usually under *Thuya*; see the "calciphile" bog succession). Occasionally this associule invades moist shale or sandstone and is more initial in nature when *Riccardia sinuata* is associated with it (Briggs Gully). The chief limiting characters of this associule appear to be high moisture conditions (usually with constant seepage required) and calcareous conditions, hence its recurrence under diverse conditions.

a. The *Trichocolea* Facies: Under less distinctly marly conditions and most often on thin soil covering north-facing talus *Trichocolea,* may occur virtually by itself or form an intergrading community between the more decidedly calciphile *Moerkia-Riccardia* Facies and the more humicole *Bazzania-Blepharostoma-Lepidozia* Associule. On the talus slopes (and even on exposed rock-fragments) at Sixmile Creek and Briggs Gully both the *Trichocolea* Facies and a *Trichocolea-Moerkia-Riccardia* Associule exist.

b. The *Riccardia-Moerkia* Facies: Under quite distinctly marly conditions (more so than evidently tolerated by the *Trichocolea*), *Moerkia* and *Riccardia* may be consociated. Like the *Trichocolea* Facies, this facies may occur either on thin soil over talus or directly on shaded, moist talus fragments as at Briggs Gully, or on springy marly, slopes as at Sixmile Creek.

2. *Fossombronia-Blasia-Anthoceros Associule.*—Occurring on loamy or clayey, locally denuded regions. This associule is rather common along paths in the Hemlock-White Pine-Yellow Birch Subclimax of the ravine slopes, but also occurs in similar paths in climax forest and on alluvial soil along the streams. It is treated separately below.

2. Occurring on rock outcrops either as pioneers or as chasmophytes.

Here persist faciations of the *Lophozia-Scapania* Associule or the more xerarch *Reboulia* Associule or further, the *Frullania-Radula-Lejeunea* Associule (see above), wherever boulders or small ledges persist. The development of a dense shade (compared with the earlier, more initial conditions) results in disappearance of many of the more light-tolerating forms as *Pellia fabbroniana, Preissia, Riccardia pinguis,* etc.

Perhaps a peculiar *Cololejeunea biddlecomiae* facies should be mentioned here. This is not a faciation of the *Radula complanata-Porella-Frullania* Facies but seemingly a distinct faciation of the *Frullania-Radula-Lejeunea* Associule, confined to shaded loose rocks lying on ravine slopes or at the

bases of the wooded talus slopes. The *Cololejeunea* occurs here on fossiliferous, porous isolated rocks and boulders, usually in pure form (rarely with *Lejeunea* accompanying it). The lack of toleration of *Cololejeunea* for direct sunlight is apparent from the luxuriousness with which the species colonizes such strongly shaded sites. Another factor that appears to favor the colonization of such low rock outcrops is the fact that the species occurs here near the ground level where the humidity is higher than at several feet above ground.

With the weathering of rock, accumulation of dense soil over the talus slopes and development of more uniform conditions, there is development of the climax forest. On the north-facing slopes this usually includes a large component of hemlock and yellow birch (in part, persistent from the subclimax) while the crests and the south-facing slopes develop a forest largely or entirely consisting of the deciduous members of the climax (e.g., beech and sugar maple). The climax forest in which hemlock plays an important part usually supports a greater variety of Hepaticae than the consociations consisting largely of either beech or maple. This appears to be due to the fact that there is less rapid accumulation of litter on the forest floor — hence a better chance for the development of societies of the ground layer. Competition here appears to be a one-sided affair between the bryophyte ground cover and the relatively rich herbaceous layer. The latter in most cases, is the deciding factor, as regards the development of bryophyte communities. In general, corticolous species such as *Radula complanata, Porella platyphylloidea, Frullania eboracensis* and *brittoniae* and such terricolous forms as *Plagiochila asplenioides, Calypogeia trichomanis,* etc., are able to survive to a considerable degree while in local sites where small rock outcrops persist, many of the saxicolous communities persist, in relatively attenuated form. On the rotting logs most of the species mentioned above survive, except those unable to stand dense shade; there is therefore a preponderance of the shade-loving or tolerating *Cephalozias* (especially *media*), *Lophocolea heterophylla* and *Ptilli-dium pulcherrimum* and to some degree *Jamesoniella* and *Odontoschisma.*

E. The Ravine-floor Communities. — When the ravine floor is elevated above the level attained by the spring floods, the corticolous, xylicolous and humicolous communities listed for the Ravine-slopes (*D.*, p. 663 and following) also occur on the ravine floors unless the valley has been broadened to such a degree that the typical deciduous forests have succeeded and the climax or a flood-plain subclimax has been attained (as is often the case near the mouths of the ravines). Where flooding occurs periodically, the hepatic flora is much more limited and very few species occur in the typical Elm-Sycamore-Ash Flood-plain Forest fringing the wider ravines. Such species as *Chiloscyphus pallescens* and *polyanthus* however, do occur there, and the var. *rivularis* of the latter may occur to the waters' edge or even submerged (Zone F and G in Fig. 12).

F. The Stream-bank Communities.

1. *Fossombronia-Blasia-Anthoceros Associule.*—On the alluvial soil at the edges of the broader or more mature ravines (or near their mouths),

occur facies of the *Fossombronia-Blasia-Anthoceros* Associule. Generally *Blasia pusilla, A. laevis, Notothylas orbicularis* and occasionally *A. punctatus* or *crispulus* and *Pellia epiphylla* are consociated into a distinct associule here. This associule is found again in various faciations on loam banks (on the moister ravine slopes) and on paths and along wagon-roads, wherever there occur highly compacted soils of a high water-retaining capacity.

In the younger, more turbulent portions of the ravines (as near the head of Sixmile Creek), another associule occurs:

2. The *Chiloscyphus polyanthus* var. *rivularis Associule.*—On the margins of narrow brooks or narrow, young ravines, occurs the above associule, usually found with *Anthoceros laevis* and *Riccardia pinguis* wherever subcalcareous conditions occur—usually on moist rocks, occasionally on moist soil. Locally very rarely, elsewhere more commonly, *Jungermannia* species and *Marsupella emarginata* occur here.

G. The Submerged Stream Communities.—A single associule, the *Porella pinnata-Chiloscyphus* Associule occurs here. The members are found with such mosses as *Fontinalis,* attached to rocks in swiftly running streams.

THE WHITE PINE-HEMLOCK-SUGAR MAPLE-BEECH-YELLOW BIRCH FOREST

Forests very similar to such a climax[74] occur as subclimaxes of bogs, as subclimax or edaphic climax; (see under "The Northern Coniferous Forest Formation" p. 650 and following). They occur on the north-facing slopes of many ravines (see under "The Hemlock Ravine Communities" p. 661 and following) but also occur widely on the north-facing slopes of the higher hills (away from the ravines where the hepatic flora is very similar to that outlined under the Hemlock Ravine communities) but with none of the epipetric species present, and in swamps. In swamps (Slaterville Swamp, Michigan Hollow Swamp, etc.) there is little or no sugar maple (replaced by red maple) and usually no beech while there is green and black ash.

In the swamps the hepatic flora is much as outlined for the subclimax of the Coniferous Forest Formation and is characterized by a large number of species among which *Calypogeia neesiana* var. *meylanii, Bazzania trilobata, Trichocolea tomentella, Harpanthus scutatus, Geocalyx graveolans* are perhaps the most frequent. The succession in swamps, from bark to humus, is traced in Fig. 13 where there are listed the more frequent and constant species to be expected under such conditions.

The hepatic flora of the hemlock and white pine containing subclimax and climax forests is decidedly richer than in the entirely deciduous forests (Beech-Maple Climax or consociations of either) which occur scattered

74 This corresponds to the climax Hemlock-White Pine-Northern Hardwood Forest of Nichols (1935) and the "Lake Forest" of Weaver and Clements (1938). It is largely limited to cooler, more elevated, usually north-facing regions.

throughout some of the Appalachian Plateau region. This appears to be due to the greater prevailing humidity (as well as a generally moister soil-surface) and the cooler climate (to which such forests are restricted) as well as the lesser density of the forest litter. The hepatic flora is, however, never as northern in facies as in the ravine communities, nor is it as rich since a greater degree of uniformity is attained, with a great reduction in the types of available niches.

MISCELLANEOUS COMMUNITIES

The Pond Communities.—The initial stages of ponds (Potamogeton-Water Lily Stage) lack any hepatic element. However, the fringing *Lemna-Spirodella-Wolffia-Ricciocarpus* Associule is characterized by the presence of one species of hepatic *(Ricciocarpus natans)* which is often an important element floating at the surface of the water. A second species *(Riccia fluitans)* floating with *Utricularia* and *Lemna trisulca* just below the water surface, forms a *Lemna trisulca-Riccia fluitans* Associule.

Around the edges of ponds in the *Arum-Saggitaria-Peltandra* Zone, these two species of Hepaticae persist as subterrestial forms. Here occasionally, other species of *Riccia* come in (*crystallina* and *sorocarpa,* etc.).

The Loam Bank, Stream Bank and Sand Plain Communities.—The above communities though occurring under diverse conditions, agree in several ways: they are limited to substrates of a friable, loose nature (hence an environment of a very unstable type) which are always low in organic materials. Furthermore, the exposed nature of the soil or sand is usually correlated with a low calcium content due to leaching. Several different hepatic associules of two basic types occur here: (1) a community of annual thallose forms, comprising mesophytes, and (2) a perennial community of xeromorphic leafy types.

1. The Mesarch Annual Communities.

a. The *Fossombronia-Blasia-Anthoceros* Associule: This has been described above (as it occurs on loam banks and stream banks (*F*) in the Ravine Slope Forests) and requires no further comment. It consists of essentially annual forms (or forms like *Blasia* that die annually except for the youngest portions of the plant) and occurs usually on clayey or loamy banks but may occur on moist alluvial soil along the edges of streams where it intergrades with the next associule.

b. The *Riccia-Ricciocarpus Associule.*—This, unlike the preceding associule, occurs only on ground subject to inundation and is therefore limited to the edges of stream banks. It consists largely of species of *Riccia* (*R. crystallina, sorocarpa, arvensis,* occasionally terrestial forms of *fluitans*) and the terrestial form of *Ricciocarpus natuans.* At times it occurs with *Anthoceros laevis* and *Notothylas orbicularis* and then grades into the previous community.

2. *The Xerarch Sand-Plain and Terrace Associule.*—This consists of two possibly distinct associules. On Sand Plains exists the xerarch *Cephaloziella-Lophozia bicrenata* Associule, similar in all regards to the xerarch Ravine-

crest Community. It occurs for example, on the acid sand plains surrounding the Junius Bogs. On exposed, dry, sandy or gravelly river-terraces and occasionally on rocky dry, insolated crests of hills, there exists a limited *Mannia fragrans* Associule. This has not yet been found in our area but has undoubtedly been overlooked.

Invasion and Succession[75]

Very little is known relative to invasion and succession by Hepaticae. Skutch (1929) and Torrey (1932, 1932a) discuss invasion by *Marchantia polymorpha* of recently burned-over areas.

Griggs (1935, 1937) recorded the invasion of Katmai Ash by *Lophozia bicrenata* and *Cephaloziella byssacea;* Sharp (1939) noted colonization of denuded clay by this society of species. The writer finds that in central New York *Lophozia bicrenata* and *C. rubella* (more rarely *byssacea*) abundantly invade denuded loamy or sandy soil, especially on banks, in sunny, exposed regions that have been leached of lime. These two species are almost invariably associated and occasionally are accompanied by other species, frequently by *Lophoceola minor* in areas where traces of lime still occur or by *Lophozia barbata;* in more acid areas as around swamps, denuded loamy soil may support this society, accompanied by *Plectocolea crenulata* and occasionally by pachydermous modifications of *Scapania irrigua.*

The moist, exposed vertical sides of cattle tracks in fields are often colonized by *Notothylas orbicularis* and *Riccia* species.

Shaded sandy-loamy or clayey, moist soil of little used paths and the middle of old wagon roads or abandoned logging roads are invaded especially by a society consisting of *Fossombronia wondraczekii, Plectocolea crenulata, Anthoceros crispulus, A. laevis* and occasionally *Blasia* and *Pellia* and *Notothylas.* Similar invasions occur on denuded banks where the moss *Pogonatum pennsylvanicum* is often a characteristic associated species; on very moist or wet banks *Blasia* is usually the dominant member, on less moist banks *Fossombronia* and *Plectocolea* are more important. The colonization of such banks appears to be an important factor in preventing washouts on roads since the mats renew themselves annually, even though they may be largely destroyed by the spring washes; on all but steep slopes this society is usually soon replaced by vascular plants among the first of which are colts-foot *(Tussilago),* species of *Epilobium (coloratum, glandulosum, molle)* and *Gratiola neglecta.*

Hepaticae are among the first species to invade flood-plains; the terrestial forms of *Riccia fluitans* and *Ricciocarpus natans* as well as *Riccia arvensis, Notothylas obicularis* and *Anthoceros laevis* are among the earliest forms to colonize moist alluvial soils.

Rocks are colonized at a relatively slow rate. Moist non-siliceous rocks are often colonized locally by *Radula complanata* and *Lejeunea cavifolia;* similar, somewhat moister rocks are colonized by *Radula obconica* and *tenax*

75 Considerable incidental data on succession is given in the preceding section, which need not be repeated here.

and *Metzgeria conjugata;* somewhat dryer rocks are most often colonized by *Cololejeunea biddlecomiae,* mostly to the exclusion of other species, forming characteristic pale yellow-green hazy overgrowths especially on loose, calcareous, often fossiliferous rocks lying in the bottom or on the steep slopes of ravines. Rather shaded and rather dry shale and sandstone rocks are occasionally invaded by *Leucolejeunea clypeata* (forming large, nearly circular patches) very rarely by *Frullania asagrayana* (usually under more exposed conditions than the *Leucolejeunea*). Siliceous rocks such as the quartz-conglomerates around Rock City, are colonized by an entirely different group of species; on moist vertical faces by *Tritomania exsecta* and *exsectiformis, Anastrophyllum michauxii, A. minuta, Bazzania denudata* and *trilobata, Jamesoniella, Diplophyllum apiculatum* and *Lophozia gracilis.*

Moist shale talus derived from non-calcareous rocks may be colonized very extensively by *Gymnocolea inflata* (Taughannock) and by *Cephalozia bicuspidata* and *Calypogeia* (Taughannock and Briggs Gully).

Crevices near the exposed crests of shale and sandstone cliffs and ledges may be colonized by *Lophozia ventricosa, Tritomaria exsectiformis, Scapania nemorosa* and *mucronata, Cephaloziella hampeana* and *byssacea.*

Sphagnum bogs are invaded soon after being covered by *Sphagnum* (before any of the ericaceous plants other than *Vaccinium oxycoccus* gain a foothold) by various members of the *Mylia* Associule. They at times, form large, pure patches with a coverage of 100% for areas several yards across, in isolated cases. The *Mylia* Associule is succeeded by *Cephalozia connivens* and *C. pleniceps* soon after the ericaceous shrubs densely shade the moor. *Pallavicinia lyellii* may then invade, often partly succeeds the *Cephalozia* society largely because of its habit of forming dense, close mats.

Wet calcareous talus or wet calcareous cliffs are often invaded by *Preissia commutata* and *Riccardia pinguis,* often accompanied by *Conocephalum.* This same society may invade marly, white, moist soil at the edges of ditches around lime-sinks as at Clark Reservation (near Jamesville), accompanied there by the locally rare *Asterella tenella;* on wet cliffs or in marly swamps (Bergen) this society is often accompanied by *Pellia fabbroniana* but *Asterella* is consistently absent.

Crevices of moist calcareous rocks are invaded by mosses such as *Gymnostomum (Hymenostylium) curvirostrum,* associated with such Hepaticae as *Lophozia badensis, Lophocolea minor, Scapania mucronata* and *S. nemorosa.* All of these Hepaticae (except the *L. badensis*) become more abundant on relatively drier ledges and crevices. The latter together with the *Gymnostomum,* is abundantly present, usually as small colonies in almost all of the ravines.

The hepatic flora associated with organic substrata is particularly rich and diverse. Intensive study of the succession pattern in this area, has resulted in the compilation of the following table (Fig. 13), illustrating invasion and succession on the hardwood, deciduous silva of the Transition Zone. The

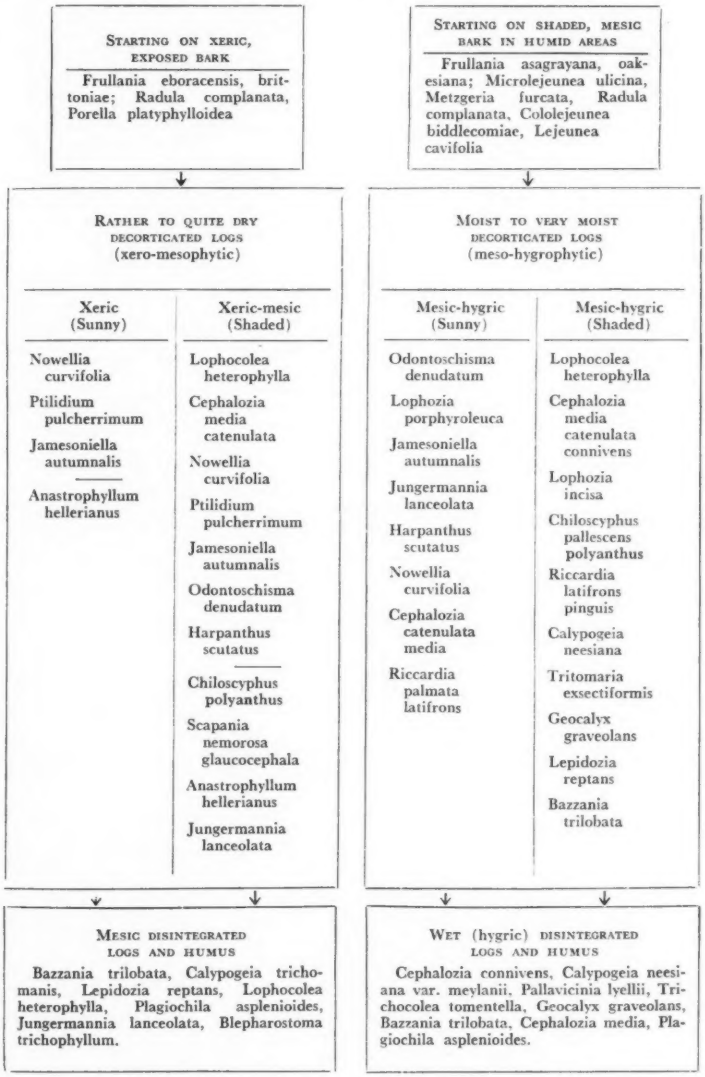

Fig. 13.—Succession from Bark to Humus in the Deciduous Forest Region

diagram is self-explanatory except in regard to the order of arrangement. The dominant species under any given set of conditions are listed first, in the approximate order of abundance (coverage as well as frequency of occurrence); rare or accessory species are listed last in a group set off from the species that are to be considered as typical members of that society. The groups here recognized are equivalent to the "Associules" of the bryoecologist; they freely intergrade when the conditions are intermediate. Not all of the species may occur in any one locality; frequently one or several associated logs and the surrounding humus layer, support the majority of the listed species.

Phytogeography[75]

The hepatic flora of the region is decidedly more similar to that of the Canadian-Hudsonian flora than to that of the Austral flora. In it occur a great number of species that can scarcely be called Transition Zone species since they are in general, so rare south of the Canadian Zone of evergreen forests that they must certainly be regarded as boreal "Canadian" or "Canadian-Hudsonian" forms.

Two general types of species occur in our area, from the floristic point of view. Firstly, those that are widely distributed, ubiquitous and occur far to our south as well as far to our north. These cannot be utilized locally, as significant species in determining the relations of our flora. The second type of species are those with a more limited distribution, finding either their northern or their southern limits in our region. These forms are certainly significant in indicating the affinities of our flora.

The species southern in distribution (i.e., "Austral" forms) that reach our borders are inconsequential here: *Frullania kunzei* and *Anthoceros reticulatus* both of which were reported from isolated stations in Cattaraugus County; these however, represent misdeterminations. The southern affinities of our flora are therefore very weak indeed. Such typical "Austral" forms as *Plectocolea fossombronoides, O. prostratum, Anthoceros carolinianus, Frullania plana,* etc. are absent.

The species occurring far to the northward and whose presence locally is to be interpreted as indicating a decided affinity with the Canadian-Hudsonian flora are much more numerous. With some exceptions, the northern forms in our area occur more or less as disjuncts or relicts. *Lophozia barbata, A. helleriana, Scapania mucronata, Lophozia badensis, L. porphyroleuca, Moerkia flotowiana, L. ventricosa, Tritomaria exsectiformis,* etc. are all rather widely distributed though limited to very local microenvironments. These species can truly be classed as Northern Transition forms, that is to say, species finding their greatest abundance and virtual limits within the Upper Transition and Canadian Zones (extending northward into the Hudsonian but not at all into the Austral). The northern forms occurring more restrictedly are *Ptilidium ciliare, Gymnocolea inflata, Lophozia marchica, Tritomaria exsecta, Scapania irrigua, S. paludicola, S. glaucocephala, S. cuspiduligera, S. sub-*

76 See the general text by Herzog (1926) in this connection.

alpina, Harpanthus flotowianus, Cephaloziella subdentata. Lophozia rutheana, Anthoceros macounii, Lophozia gracilis, Bazzania denudata, B. tricrenata, A. michauxii, Jungermannia tristis and *J. caespiticia.* These species occur so rarely elsewhere in the Transition Zone that they should be classed as Canadian-Transition or distinctly Canadian forms. *Scapania cuspiduligera, S. subalpina* and *Harpanthus flotowianus* indeed, are more characteristically Hudsonian and Arctic-alpine species. These occur in the Canadian Zone only exceptionally and appear to be unknown from elsewhere in the Transition.

The northern species in our flora may therefore be grouped in three series, each indicating progressively more northern affinities. The first, indicating Canadian-Transition affinities (in the sense used by Bray, 1930); the second, indicating Canadian or Canadian-Hudsonian affinities; the third, indicating Hudsonian affinities.

I	II	III
Ptilidium ciliare	*Gymnocolea inflata*	*Harpanthus flotowianus*
Cephalozia elachista	*Anastrophyllum minuta*	*Scapania subalpina*
Lophozia barbata	*Tritomaria exsecta ?*	*Scapania cuspiduligera*
Anastrophyllum hellerianus	*Scapania paludicola*	*Lophozia rutheana*
Lophozia badensis	*Scapania apiculata*	*Cephaloziella subdentata*
? Lophozia marchica	*Scapania glaucocephala*	*Lophozia alpestris*
Lophozia porphyroleuca	*Scapania mucronata*	
Tritomaria exsectiformis	*Anthoceros macounii*	
Scapania irrigua	*Lophozia gracilis*	
Cladopodiella fluitans	*Lophozia longidens*	
Pellia fabbroniana	*Anastrophyllum michauxii*	
Moerkia flotowiana	*Bazzania denudata*	
Lophozia ventricosa	*Bazzania tricrenata*	
Lophozia excisa	*Jungermannia caespiticia ?*	
Marsupella emarginata	*Frullania tamarisci ?*	
Mylia anomala		

I believe that the species in Group I can be used as indicators for a "Northern" Transition Climate with a frost-free period of 140 days or less. This is the climate in which black spruce *(Picea mariana),* fir *(Abies balsamea)* and larch *(Larix americana)* persist in isolated stands and where the *Sphagnum* bog Vacciniaceae *(Ledum, Chamaedaphne, Andromeda)* and *Sorbus americana* occur as occasional individuals. In this zone, tulip tree, tupelo *(Nyssa sylvatica)* and scarlet oak become very occasional or rare.

I believe that the species in Group II can be used as indicators of a "Canadian" Climate, in most cases with a frost-free period of 110 days or less. The species occur obviously as isolated disjuncts in regions where the growing season is 10-20 days longer per year. The general distribution of these species is probably north of the line where the frost-free period is less than 110 days per year.

The species in Group III occur only as very great exceptions in areas where the frost-free period is greater than 90 days per year. The occurrence of three of these species in Cattaraugus County in localities where the growing season averages about 100 days per year, is therefore truly remarkable. The

very disjunct distribution of these species south of the "Hudsonian" Zone indicates that these are truly subarctic species.[77]

The hepatic flora of the region lacks all of the so-called "Atlantic" species (isolated southern forms occurring as disjuncts far to the north) with the exception of *Microlejeunea ulicina*, occurring here as a rarity. Such forms as *Calypogeia arguta (Sullivantii), Lejeunea patens*, etc. are absent.

At the same time, the endemics so characteristic of the southern Appalachians do not reach this far north. It therefore follows that the hepatic flora locally is a flora composed of ubiquitous, widely distributed forms occurring southward throughout the Transition and often into the Austral or Subtropical Regions, typified by *Lophozia mildeana, Lophocolea heterophylla, Scapania nemorosa, Bazzania trilobata*, etc., and a series of species of obviously northerly affinities. These northern species (listed above) comprise a relict flora dating back to glacial times, much of which appears to have disappeared (perhaps largely during the dry xerothermic period) or is still disappearing (largely incidental to the colonization of the area by man). Certainly the very disjunct distribution of many of the forms and the extremely limited niches they are locally confined to, indicate that they are now retaining but a precarious foothold in our area.

GLOSSARY[78]

Acuminate—gradually narrowed to a point (as lobes of underleaf, pl. 10, fig. 12).

Air-chambers—generally polygonal cavities within the thallus, each usually opening to the dorsal surface by a pore (indicated as reticulations of thallus, pl. 16, fig. 4).

Amphigastria—underleaves (the third, ventral row of leaves, usually much smaller than the lateral rows) (pl. 1, figs. 6, 9; pl. 10, figs. 5, 10, 12; pl. 14, figs. 1, 6-9).

Androecium—the male "inflorescence": the structure bearing and including the antheridia (pl. 4, fig. 9; pl. 10, figs. 1, 6, 12).

Antheridiophore—the disk-like, stalked structure of some Marchantiales bearing groups of antheridia.

Antheridium—the male reproductive organ, usually globose or elliptical, and on a short stalk.

Antical—pertaining to the upper or dorsal surface (or margin) of the stem or leaf (opposite of postical).

Apiculate—with a sharp point (as in leaf lobes, pl. 13, fig. 3.

Appressed—flatly pressed against.

Approximate—close together (as the leaves in pl. 2, fig. 12).

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77 The orientation of the hepatic flora with that of the more northern Coniferous Region is not surprising; neither is the lack of "Austral" species. Historically, there is an excellent basis for such an orientation since the postglacial northward migration of the Tundra and Coniferous Floras might be expected to result in localized survival of northern species in small isolated pockets. On the other hand, the time factor as well as climatic reasons, make it quite understandable why there is virtually no Austral element in the Hepaticae of this region.

78 In order to make this list more useful, the terms, so far as possible, are illustrated by figures which are cited after the definition. Only terms of uncommon use outside the field of botany are defined.

Archegoniophore—the umbrella-like stalked structure of most Marchantiales, bearing groups of archegonia (pl. 16, fig. 4; pl. 17, fig. 6).

Archegonium—the female reproductive organ, each containing a single egg, more or less flask-shaped.

Areolae—small angularly shaped areas, as on the surface of a spore.

Bifid—split into two parts to a point near the base (underleaves, pl. 10, fig. 12).

Bipinnate—twice pinnate (thallus, pl. 15, fig. 2; pl. 1, fig. 10).

Bracteoles—the underleaves directly below the perianths or androecia, usually larger than normal underleaves (pl. 10, fig. 2; pl. 3, fig. 3; pl. 6, fig. 3).

Bracts—modified leaves (usually larger) at the base of the perianth (perichaetial bracts, pl. 6, figs. 3, 6) or forming a sac in which the antheridia are found (perigonal bracts, pl. 4, fig. 9; pl. 10, figs. 1, 12; pl. 11, fig. 9).

Caducous—falling off at a predetermined line of dehiscence.

Calcicolous—growing on lime-containing rock or soil.

Calciphilous—with a preference for lime-containing rock or soil.

Calciphobous—with a lack of toleration for lime-containing rock or soil.

Calyptra—the protective sheath over the immature sporophyte, developed from the archegonium-wall (pl. 10, fig. 6, within perianth).

Canaliculate—channelled or with the two edges loosely folded over each other (then canaliculate-concave) (pl. 9, fig. 8, the leaves).

Capillary—hair-like (leaf-margins, pl. 1, figs. 1, 7, 8-10).

Capitate—developed into a swollen, head-like structure.

Capsule—the spore-bearing, brownish, terminal part of the sporophyte.

Carinate—keeled (pl. 13, fig. 11k; pl. 11, fig. 6a).

Carpocephalum—the erect, stalked gametophytic structure of many Marchantiales, bearing either antheridia or archegonia (a collective term for antheridiophores and archegoniophores) (pl. 16, fig. 4; pl. 17, fig. 6).

Chlorophyllose—containing perceptible numbers of chloroplasts, imparting a green color.

Ciliate—bearing hair-like, capillary processes (pl. 1, fig. 4-10).

Collenchymatous—with the walls of the cells thickened at the angles (pl. 1, fig. 3; pl. 13, fig. 2; pl. 12, fig. 10).

Columella—the filamentous central strand of the capsule of the Anthocerotales (pl. 18, fig. 8, the central filament between the capsule-valves at the right).

Complicate—folded over each other (leaves, pl. 9, fig. 8.)

Complicate-bilobed—leaves divided into two lobes that are folded over each other (pl. 9, fig. 8).

Compressed—flattened (if from the sides, laterally, if from the top and bottom, dorsiventrally) (perianth, pl. 13, fig. 1).

Connate—grown together (bracts, pl. 4, fig. 7).

Connivent—with the distal parts (as the lobes of a leaf) perceptibly approaching each other (leaf-lobes, pl. 3, figs. 2, 7).

Cordate—heart-shaped, with the base emarginate.

Cortex—the peripheral layer of cells of the stem.

Cortical—pertaining to the outermost layer (or layers) of stem cells.

Costa—the median "vein" of the thallus (corresponding largely to the stem of leafy forms) (pl. 15, figs. 6, 8, 9).

Crenulate—with minute rounded teeth on the margins or apices (perianth mouth, pl. 5, figs. 6, 9).

Crisped—crispate, curled and wavy (leaves, pl. 9, fig. 1).

Cuticle—the outer, hard covering layer of leaves and stems.

Decurrent—the base (of a leaf), running down the stem as a sort of wing (pl. 3, figs. 2, 7).

Dentate—toothed (pl. 13, fig. 8).

Dichotomous—forking equally into two branches (pl. 2, fig. 2).

Dioecious—with antheridia and archegonia on separate plants.

Distant—far from each other (leaves, pl. 4, figs. 7, 12).

Divergent—spreading from each other (as the lobes of a leaf, pl. 4, fig. 11).

Dorsal—pertaining to the upper or antical surface.

Dorsiventral—growing in two planes, i.e., flattened, like the thallus.

Elaters—small, unicellular bodies with spiral, brownish bands, mixed with the spores in the capsule.

Emarginate—with a notch at the end, deeper than retuse and less deep than in bilobed (pl. 11, fig. 7).

Endogenous—growing or proliferating from the inside of the stem.

Entire—without trace of teeth or lobes (leaves, pl. 10, fig. 1, 7).

Epidermis—the outer layer of cells of the thallus.

Erect-spreading—erecto-patent, spreading form the stem at an angle of 45 degrees or less (upper leaves, pl. 8, fig. 1; pl. 4, fig. 1).

Erose—worn away irregularly (like the leaf-margins in gemmae-formation, pl. 10, fig. 9).

Explanate—spreading out (most lobules in pl. 14, fig. 8).

Exserted—projecting beyond surrounding parts (such as perianth beyond bracts, as in pl. 7, fig. 16).

Falcate—somewhat curved, like a sickle.

Filiform—thread-like (shoots, pl. 7, fig. 8).

Flagellae—whip-like, slender, largely leaf-less, stem-like structures (see *stolons*).

Flagelliform—flagellae-bearing; bearing slender, whip-like structures.

Foliose—leaf-like, leafy (plates 1-14).

Fusiform—equally tapering at both ends, spindle-shaped (capsules, pl. 18, fig. 7).

Gametophyte—the green, prominent generation of bryophytes, the "plant" bearing on it the sexual organs and sporophyte.

Gemmae—small vegetative reproductive organs, often of 1-2 cells borne by the gametophyte (pl. 7, figs. 6, 15; pl. 4, fig. 8).

Gemmiparous—gemmae-bearing (pl. 10, fig. 9; pl. 11, fig. 1; pl. 8, fig. 7).

Geniculate—bent like a knee.

Guttulate—pertaining to cells when the lumen appears like a rounded drop because the cell walls have become thick and prominent (pl. 8, fig. 14).

Hyaline—transparent, bearing few chloroplasts.

Hydrophyte—a plant growing submerged in the water or floating on it.

Hygrophyte—a plant growing on soil or rocks saturated by water or kept moist by seepage.

Imbricate—closely approximated and overlapping (like the tiles of a roof) (leaves in pl. 8, fig. 17).

Incised—cut sharply, with a narrow, acute sinus (underleaves, pl. 10, fig. 12).

Incubous—leaves inserted so that the dorsal (antical) margin overlaps (or lies above) the posterior (ventral or postical) margin of the leaf in front of it. The leaves thus have their *upper* edge nearest the apex of the shoot. The opposite of succubous (pl. 2, fig. 8; pl. 1, fig. 4).

Insertion—the place or line along which a leaf is inserted on the stem.

Intercalary—situated between the base and the growing point of a shoot.

Involucral bracts—the uppermost pair of leaves, when they sheath the base of the perianth (pl. 6, fig. 3; pl. 3, fig. 3).

Involucre—a short, incomplete or complete tube or sheath protecting the immature sporophyte or archegonia (usually formed by the uppermost pair of leaves) (pl. 6, fig. 3; pl. 11, fig. 6d).

Keel—a ridge, like the keel of a boat (pl. 13, fig. 11k).

Laciniate—deeply, irregularly divided (pl. 3, figs. 1, 3).

Lacunose—bearing pits or irregular depressions, full of holes (pl. 17, fig. 3).

Lamina—the thin wings on each side of the "vein" of the thallus; the blade of a leaf (pl. 18, fig. 3).

Lanceolate—narrow and pointed like a lance-head, like ovate but narrower and more pointed (leaf-lobes, pl. 6, figs. 7, 8).

Ligulate—lingulate, tongue or strap-shaped (thallus, pl. 15, fig. 8).

Lobe—that part of the leaf *distad* of the point to which the leaf is divided.

Lobule—the small, usually inflated ventral "lobe" or lower half of the leaf, bent under and concealed by the larger, upper half of the leaf (pl. 14, figs. 1-10).

Lumen—the cell cavity.

Medulla—the interior, non-cortical part of the stem (usually consisting of thinner cells).

Mesophyte—plants growing under moderate, little intermittent conditions of moisture.

Midrib—the "vein" of the thallus, or costa (pl. 18, fig. 3; pl. 15, fig. 9).

Monoecious—the antheridia and archegonia on the same plant includes both autoecious when these occur on different branches, and pareoecious when they occur on the same shoot (with the antheridia in the axils of the bracts below the perianth).

Mucronate—abruptly pointed with a sharp, tooth-like process (pl. 13, fig. 12).

Muriculate—with small, sharp wart-like protuberances (pl. 18, fig. 5).

Mycorrhizal—associated with fungi in a symbiotic relationship.

Obtuse—with the apex more than 90 degrees and often more or less rounded (pl. 12, fig. 5; pl. 13, fig. 11).

Ocelli—large, discolored (usually deeper colored) cells in the leaf (pl. 14, fig. 3).

Ovate—nearly egg-shaped (leaf, pl. 2, fig. 6).

Palmate—divided like a hand into finger-like lobes (pl. 15, figs. 3, 7).

Papillae—minute protuberances.

Paroecious—see *Monoecious*, with antheridia on the same shoot below the archegonia (pl. 11, fig. 9).

Patent—spreading (at more than 60 degrees) (pl. 10, figs. 1, 9).

Pectinate—comb-like (leaf insertion, pl. 9, fig. 8).

Perianth—a tube-like sheath, usually constricted at the apex, that surrounds the calyptra and young sporophytes (or archegonia) (pl. 1, fig. 1; pl. 11, fig. 6c; pl. 14, fig. 9).

Perichaetial bracts—the bracts below the perianth, "involucral bracts" (pl. 6, figs. 3, 6; pl. 8, fig. 17; pl. 11, fig. 6d).

Perigonal bracts—the bracts in the axils of which the antheridia occur, the "male" bracts (pl. 11, fig. 9; pl. 8, fig. 4).

Perigynium—a fleshy, tubular structure (replacing, more or less, the perianth), within which the sporophyte develops.

Pinnate—branching like a feather (pl. 14, fig. 2; pl. 1, fig. 2).

Plicate—bearing folds or pleats (perianth, pl. 8, figs. 2, 17).

Pores—openings through the epidermis into the air-chambers of the Marchantiales (pl. 16, figs. 1, 2, 5, 7).

Postical—pertaining to the under or ventral side.

Pseudoelaters—small sterile cells, often angular and bent, that lack a regular spiral thickening band (pl. 18, figs. 4, 6, 10).

Pseudoperianth—the perianth-like structure or sheath around the calyptra in the thallose liverworts, not obviously originating from the union of three leaves (pl. 15, fig. 5).

Reticulate—with a net-work (pl. 17, fig. 4; pl. 16, fig. 6).

Retuse—with the apex shallowly, obtusely emarginate (pl. 10, fig. 11, the leaf on the left).

Rhizoids—unicellular filamentous structures serving to anchor the gametophyte to the substrate (pl. 10, figs. 5, 10).

Rostellate—with a beak (pl. 9, fig. 3; pl. 11, fig. 9).

Saccate—like a small sack, or bearing a small sac.

Scale—a flat, unistratose appendage (pl. 16, fig. 3; pl. 17, fig. 2).

Secund—turned to one side, as if wind-blown.

Serrate—toothed like a saw (pl. 13, figs. 12, 14, the leaf-tips).

Sheathing—clasping snugly.

Sinuate—with a wavy edge or margin (bracts, pl. 5, fig. 1; pl. 11, fig. 6d).

Sinus—the emargination or "cut," as between the lobes of a leaf.

Spore—the small reproductive bodies found within the capsule (pl. 17, figs. 4-5; pl. 18, figs. 2, 5, 9).

Sporophyte—the asexually reproducing generation, consisting at most of attaching foot, a seta or stalk and a capsule, always attached to the green gametophyte (pl. 11, figs. 6a and b).

Squarrose—spreading at 90 degrees or slightly more (if much more, then recurved) (pl. 8, fig. 7, lower leaves).

Stellate—star-shaped (pl. 8, figs. 5, 16).

Stolon—a creeping stem with minute, reduced leaves (pl. 3, fig. 8).

Stoma, stomata—the modified pores of Anthocerotales, each surrounded by a pair of sausage-shaped "guard-cells" (pl. 18, fig. 11).

Subinvolucral bracts—the lower pair or pairs of bracts below the terminal bracts sheathing the perianth (pl. 5, fig. 7).

Succubous—the type of leaf-insertion where the antical (dorsal) leaf-margins lies above the leaf-margin of the leaf directly behind it; i.e., the leaves are shingled so that the upper leaf-margins are nearer the base of the stem, not nearer the apex (pl. 7, fig. 1; pl. 10, figs. 1, 7; pl. 11, figs. 1, 9).

Terete—cylindrical and smooth (perianth, pl. 9, fig. 3; pl. 11, fig. 9).

Thallus—a plant body not differentiated into leaves and stem; frond-like and flat (pls. 15-18).

Trigones—the thickenings at the angles of cells (pl. 1, fig. 3; pl. 13, fig. 2).

Trigonous—bearing three angles (perianth, pl. 3, fig. 8).

Truncate—abruptly and squarely cut-off (leaves, pl. 10, fig. 6; perianth, pl. 11, fig. 9).

Tuberculate—bearing warts or papillae.

Underleaves—the lower, ventral or postical row of leaves (usually smaller than the lateral), the amphigastria (pl. 4, figs. 6, 7; pl. 7, figs. 1, 7, 13; pl. 14, figs. 1-3).

Undulate—wavy (thallus, pl. 15, fig. 5; leaves, pl. 9, fig. 1).

Uniseriate—arranged in a row of single cells (leaf-lobes, pl. 1, fig. 1).

Unistratose—arranged in a plane one cell thick (lamina, pl. 18, fig. 3).

Valve—one of the divisions of the capsule (pl. 18, fig. 8; pl. 11, fig. 6a).

Ventral—pertaining to the lower or under-side.

Verrucose—covered with wart-like papillae.

Xerophytic—adapted to a habitat with a very intermittent water-supply.

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EXPLANATION OF PLATES

All of the illustrations (except two, properly accredited) were drawn by the writer from living material or from glycerine-jelly slides. All figures dorsal view unless the contrary is noted.

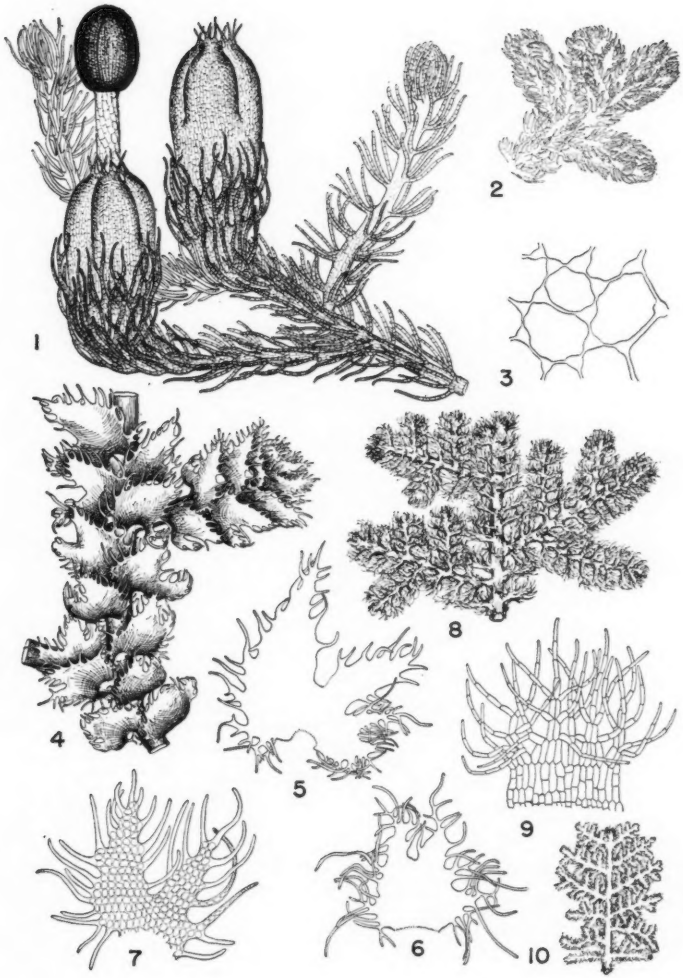

Plate 1. Figs. 1-10.—1. *Blepharostoma trichophyllum* (part of fertile shoot). 2, 3, 7. *Ptilidium pulcherrimum* (2, part of sterile shoot; 3, cells of base of leaf-lobe; 7, leaf outline). 4-6. *Ptilidium ciliare* (4, part of sterile shoot; 5, leaf outline; 6, underleaf). 8-10. *Trichocolea tomentella* (8, apex of sterile shoot; 9, underleaf; 10, habit sketch of plant).

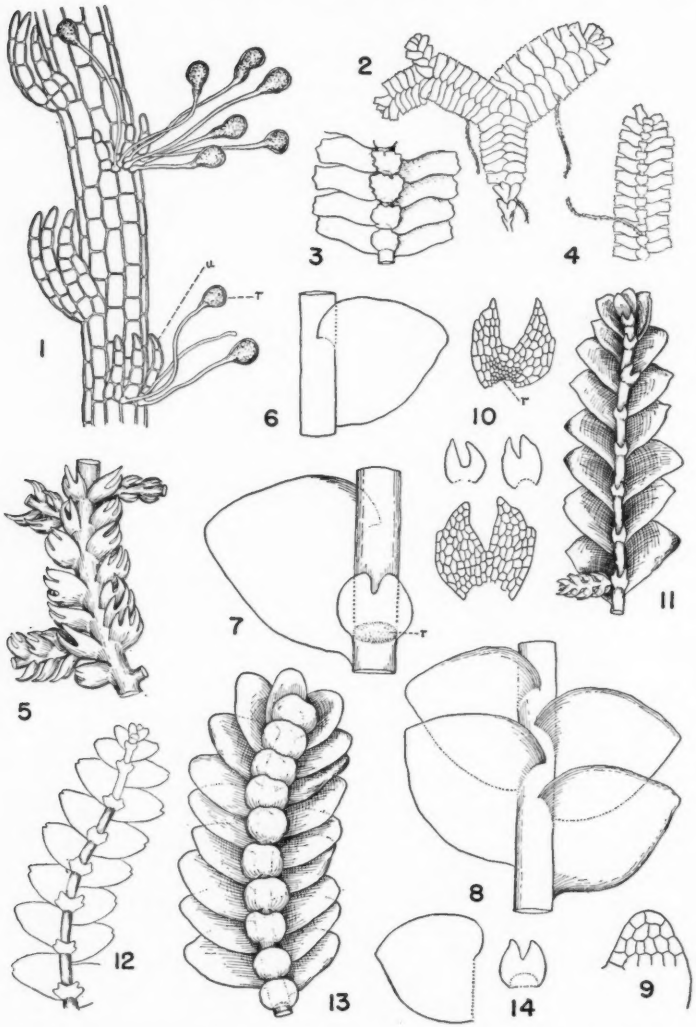

Plate 2. Figs. 1-14.—1. *Microlepidozia setacea* (part of sterile shoot, latero-ventral view, showing underleaves and mycorrhizal fungal infestation, and two lateral leaves). 2-4. *Bazzania trilobata* (2, dorsal view of shoot; 3, 4, ventral views of shoots). 5. *Lepidozia reptans* (dorsal view of portion of shoot). 6-9. *Calypogeia mülleriana* (6, leaf, dorsal view; 7, leaf and underleaf, ventral view; 8, dorsal view of part of shoot; 9, apex of underleaf shown in fig. 7). 10, 11. *Calypogeia sphagnicola* (10, four underleaves, the rhizoid-initial region (*r*) indicated on one; 11, ventral view of shoot, with postical androecium). 12. *Calypogeia fissa* (ventral view of shoot, with rhizoid initial region omitted). 13. *C. neesiana* (ventral view of shoot.) 14. *C. trichomanis* (Leaf and underleaf, after Müller, 1947).

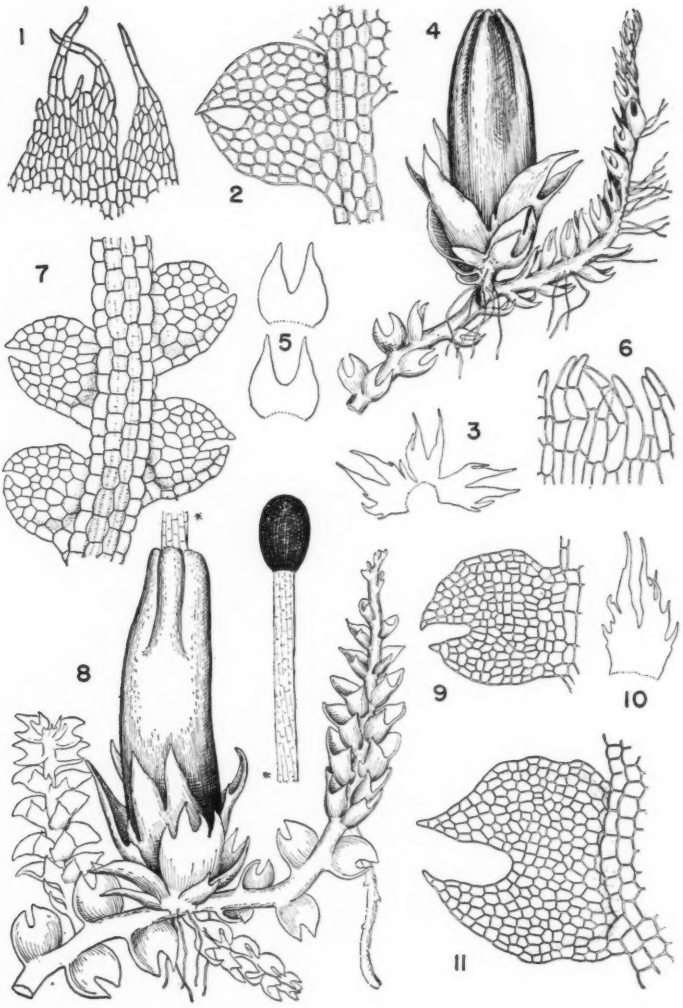

Plate 3. Figs. 1-11.—1-3. *Cephalozia connivens* (1, part of perianth mouth; 2, leaf; 3, bracts, with bracteole between). 4-6. *C. bicuspidata* (4, fertile plant; 5, two mature leaves; 6, cells of perianth mouth). 7. *C. media* (part of sterile shoot). 8, 9. *C. pleniceps* (8, fertile plant with perianth and androecia; 9, leaf). 10, 11, *C. macrostachya* (10, female bract; 11, leaf).

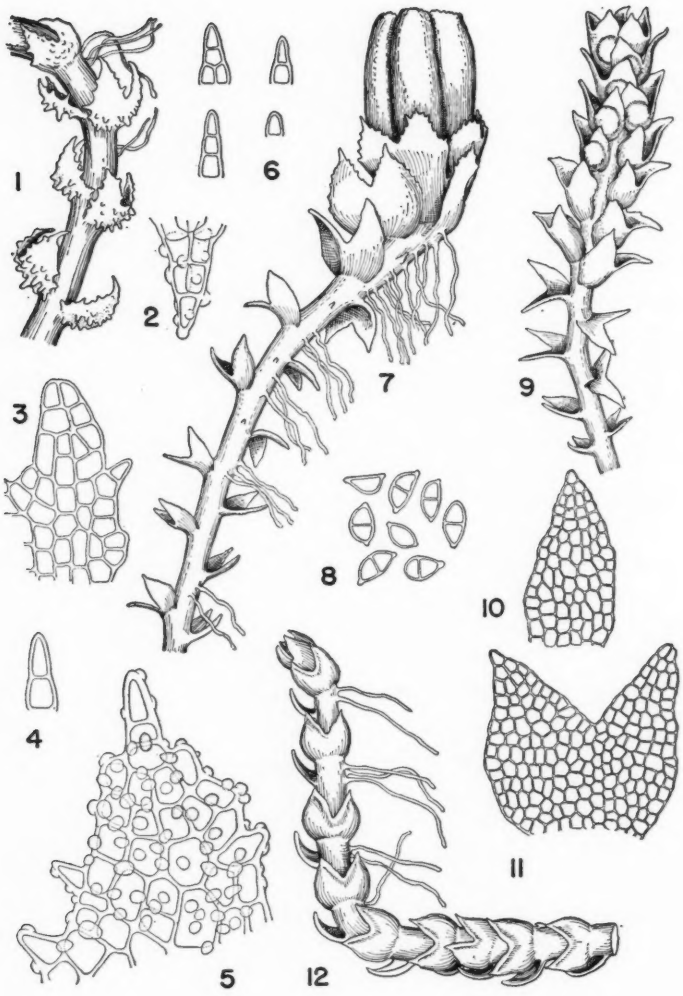

Plate 4. Figs. 1-12.—1-5. *Cephaloziella byssacea* var. *scabra* (1, part of shoot; 2, cellular "papilla" from back of leaf; 3, half of large underleaf; 4, small underleaf; 5, leaf-lobe, showing cuticular papillae). 6-9. *Cephaloziella hampeana* (6, four underleaves from fertile shoots; 7, female shoot; 8, gemmae; 9, male shoot). 10-12. *Cephaloziella byssacea* (10, underleaf; 11, leaf; 12. sterile shoot).

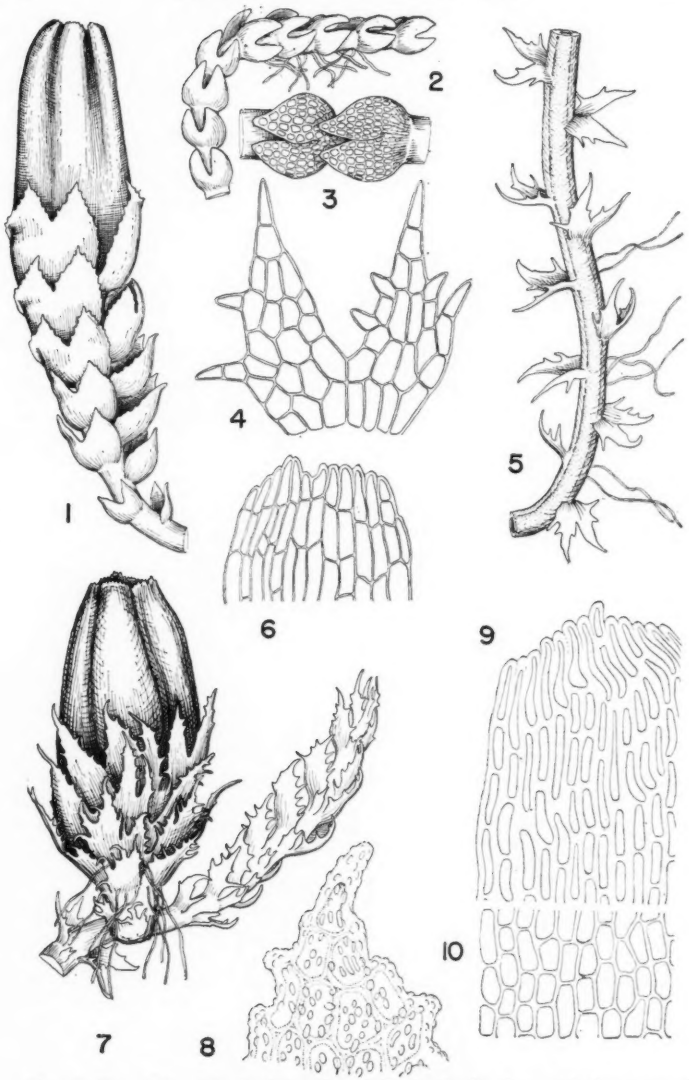

Plate 5. Figs. 1-10.—1-3. *Cephaloziella rubella* (1, fertile plant, with four pairs of male bracts below the perianth; 2, part of sterile shoot, lateral view; 3, small part of shoot, showing thick-walled cells and transverse leaf-insertion). 4-7. *Cephaloziella elachista* (4, leaf; 5, sterile shoot; 6, lobe of perianth-mouth; 7, fertile shoot with perianth and androecium). 8-10. *Cephaloziella subdentata* (8, apical part of bract; 9, perianth-mouth; 10, cells of middle of perianth).

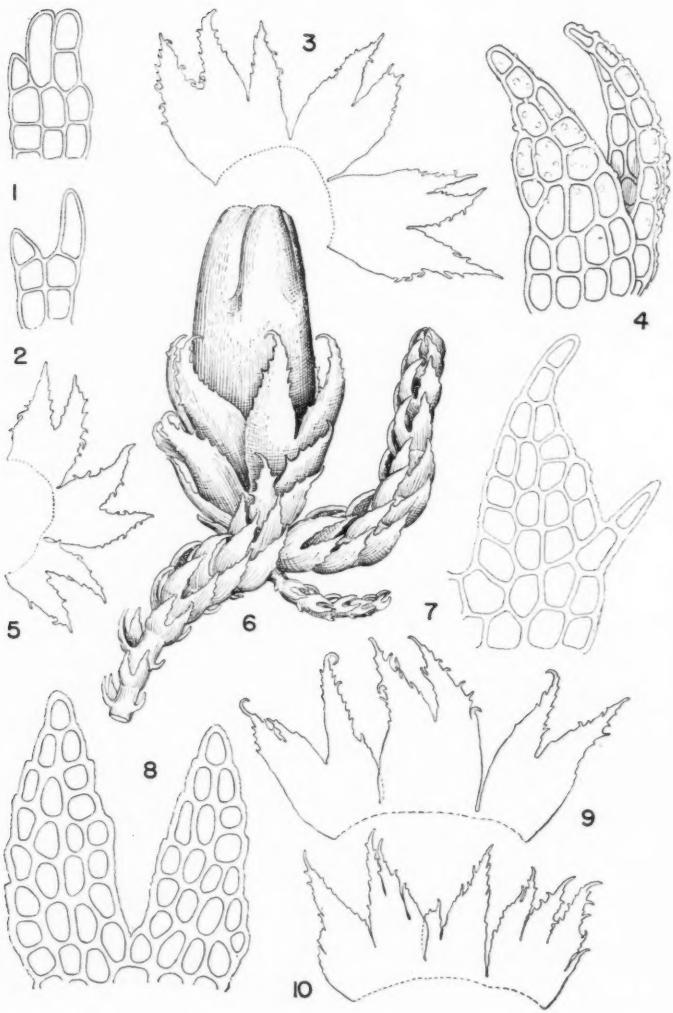

Plate 6. Figs. 1-10.—*Cephaloziella subdentata* (all from material from Bergen) (1, large underleaf from sterile shoot; 2, same; 3, ring of female bracts; 4, leaf; 5, ring of bracts; 6, female shoot; 7, half of leaf; 8, leaf of pachydermous modification, with cuticular papillae not drawn in; 9, 10, bracts).

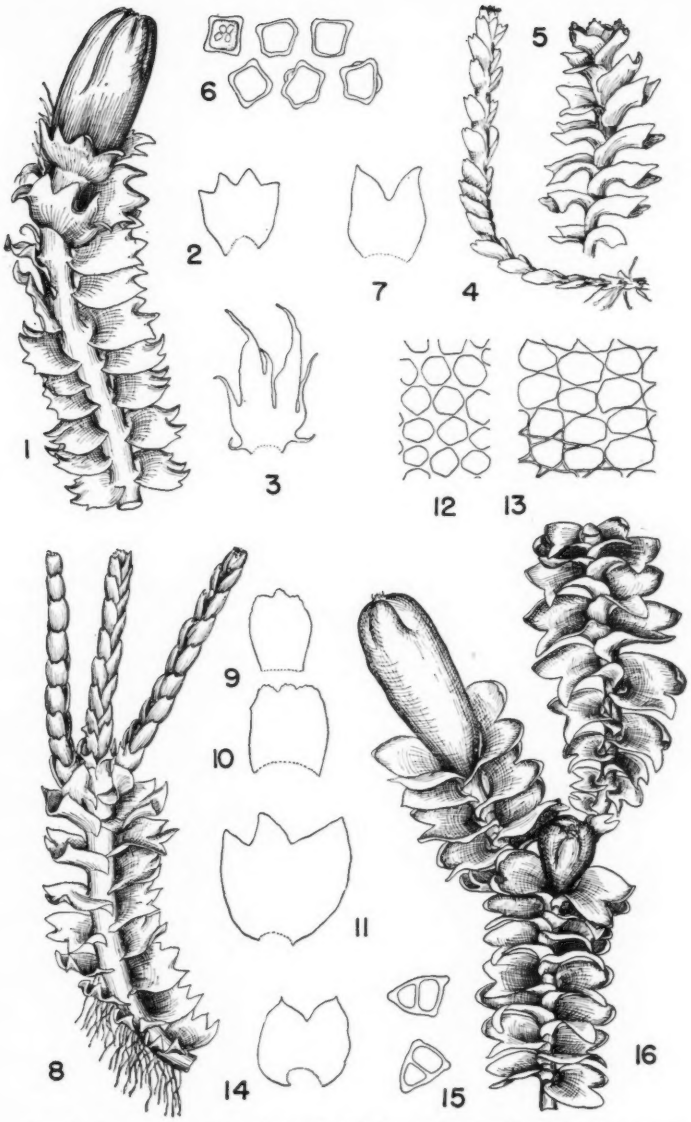

Plate 7. Figs. 1-16.—1-3. *Lophozia* (*Barbilophozia*) *barbata* (1, fertile plant; 2, normal leaf; 3, underleaf from apex of fertile shoot). 4-7. *Anastrophyllum* (*Crossocalyx*) *hellerianus* (4, gemmiparous shoot; 5, nearly normal vegetative shoot; 6, gemmae; 7, leaf). 8-11. *Lophozia* (*Orthocaulis*) *attenuatus* (= *gracilis*) (8, gemmiparous sterile shoot; 9, 10, gemmiparous leaves; 11, normal leaf). 12-16. *Anastrophyllum* (*Euanastrophyllum*) *michauxii* (12, cells near leaf apex; 13, cells near leaf-middle; 14, leaf; 15, gemmae; 16, fertile plant).

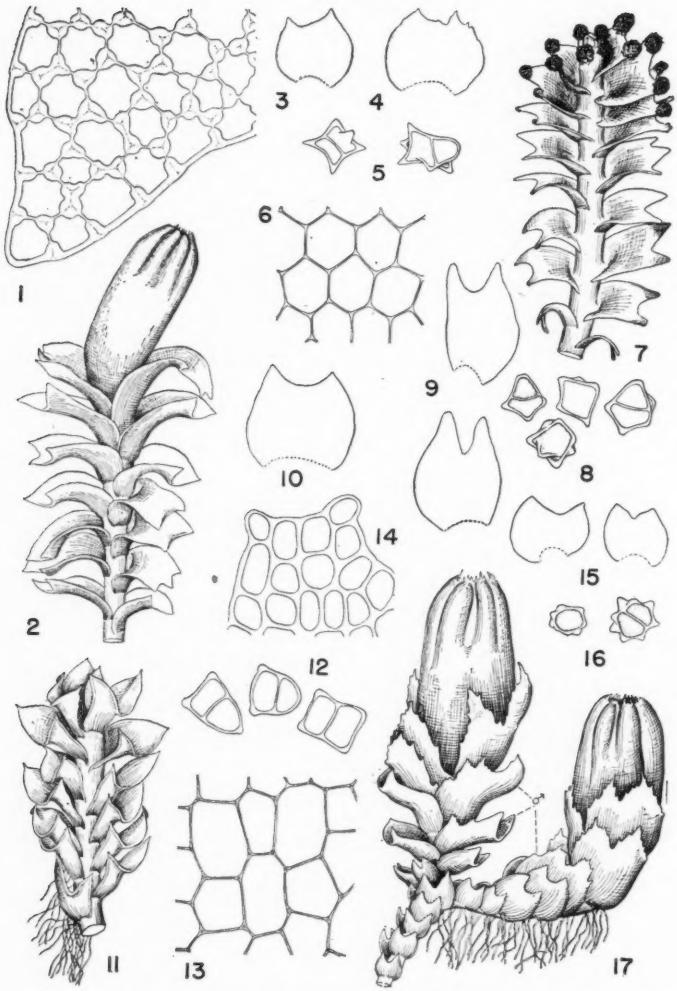

Plate 8. Figs. 1-17.—1, 2. *Lophozia* (*Dilophozia*) *porphyroleuca* (1, cells of lobe; 2, fertile shoot). 3-6. *Lophozia* (*Dilophozia*) *excisa* (3, leaf; 4, male bract; 5, gemmae; 6, cells of leaf-middle). 7-9. *Lophozia* (*Dilophozia*) *longidens* (7, gemmiparous shoot; 8, gemmae; 9, two leaves). 10. *Lophozia* (*Dilophozia*) *ventricosa* (10, leaf). 11-13. *Lophozia* (*Massula*) *incisa* (11, small, underdeveloped shoot of a modification *pachyderma;* 12, gemmae; 13, leaf-cells). 14-17. *Lophozia* (*Isopaches*) *bicrenata* (14, cells of apex of gemmiparous leaf; 15, two leaves; 16, gemmae; 17, fertile plant with male bracts below female).

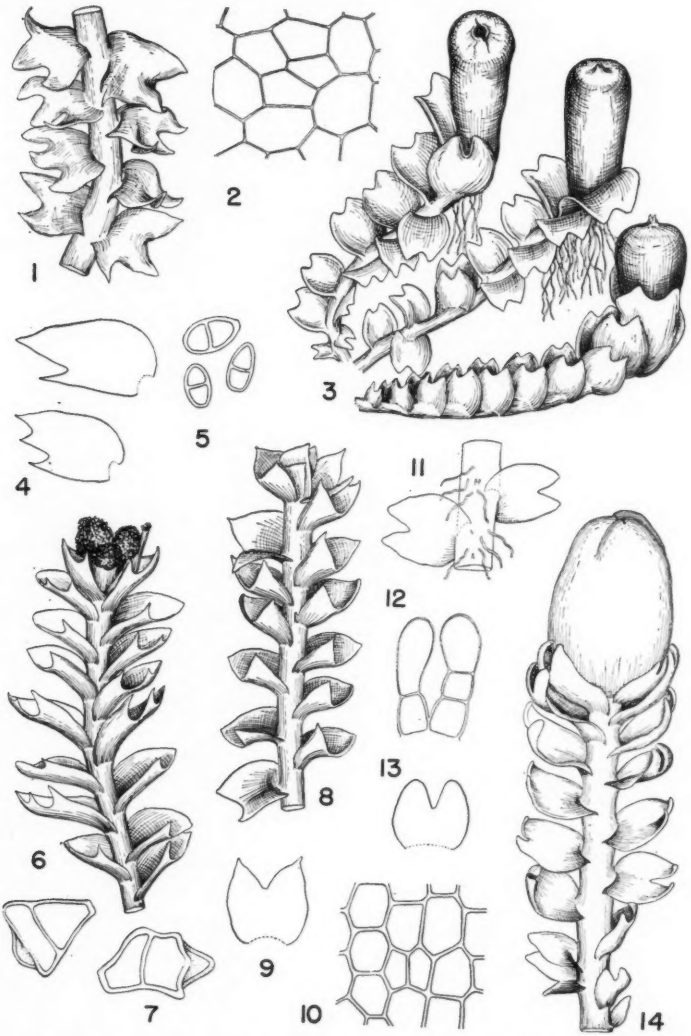

Plate 9. Figs. 1-14.—1. *Lophozia* (*Massula*) *marchica* (sterile shoot). 2, 3. *Lophozia* (*Leiocolea*) *badensis* (2, cells of leaf-middle; 3, fertile plants). 4-6. *Tritomaria exsecta* (4, two leaves; 5, gemmae; 6, gemmiparous shoot). 7. *Tritomaria exsectiformis* (gemmae). 8-10. *Anastrophyllum* (*Sphenolobus*) *minutus* (8, sterile shoot; 9, leaf; 10, cells). 11-14. *Gymnocolea inflata* (11, ventral view of shoot, showing scattered rhizoids and minute underleaves; 12, underleaf; 13, female bract; 14, plant bearing a caducous perianth).

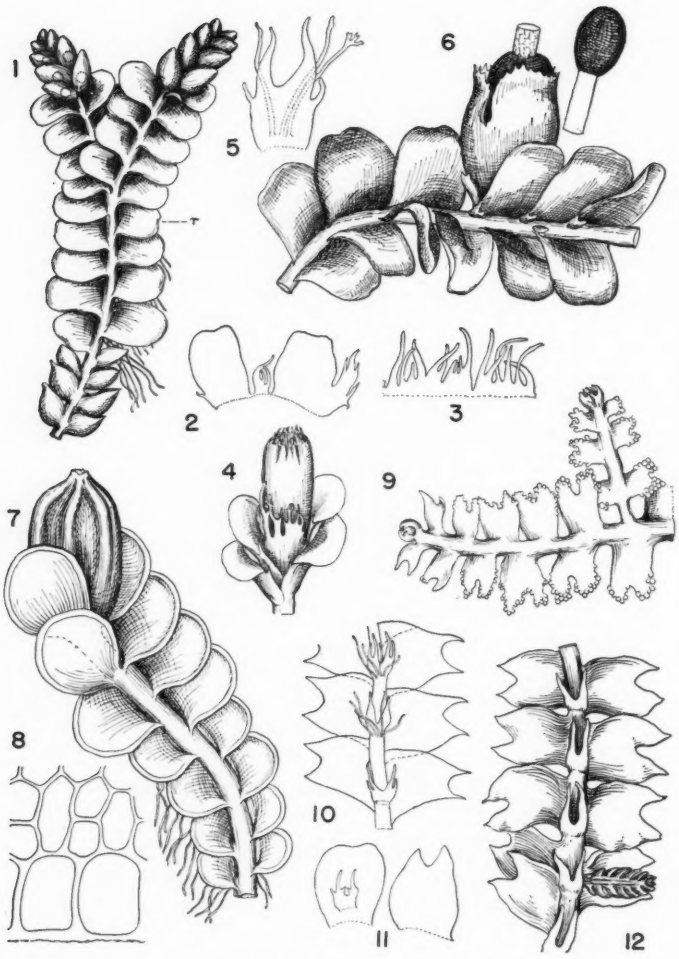

Plate 10. Figs. 1-12.—1-4. *Jamesoniella autumnalis* 1, (male shoot, showing androecia; 2, female bracts with bracteole in center; 3, apex of perianth; 4, perianth and bracts). 5. *Chiloscyphus polyanthus* (underleaf, showing rhizoid initial region at its base). 6. *Chiloscyphus pallescens* (fertile plant). 7, 8. *Plectocolea crenulata* (7, fertile shoot; 8, leaf-cells, the marginal ones below). 9. *Lophocolea minor* (dorsal view of gemmiparous shoot). 10. *Lophocolea bidentata* (ventral view of part of shoot, showing rhizoid initial region at base of underleaves). 11. *Lophocolea heterophylla* (upper leaf at left, lower leaf at right, underleaf). 12. *Geocalyx graveolans* (ventral view of shoot, rhizoids omitted, showing postical androecia).

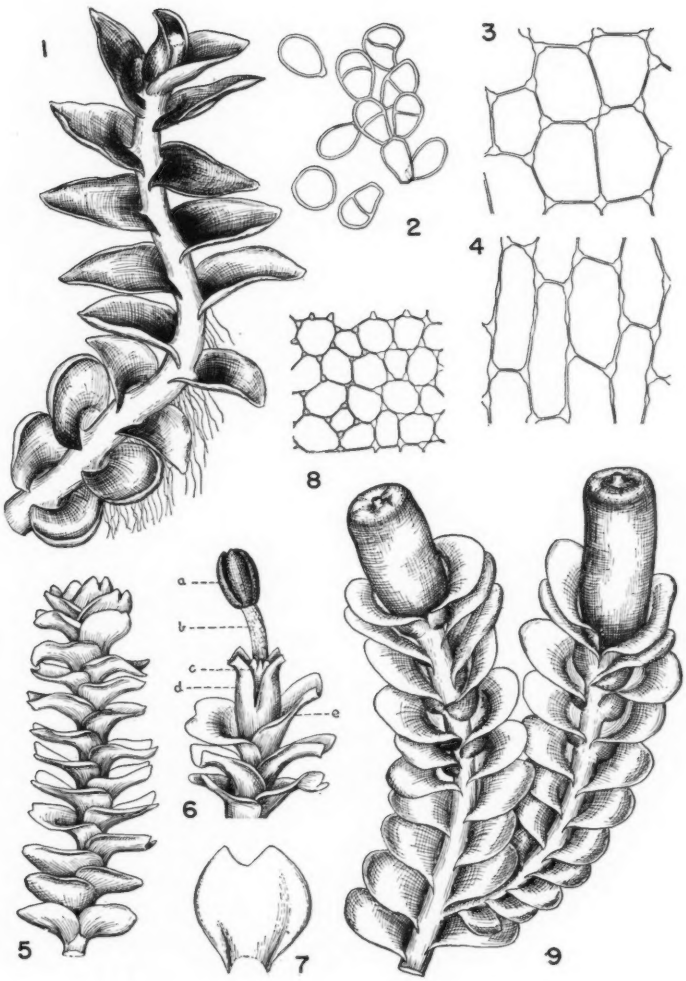

Plate 11. Figs. 1-9.—1-4. *Mylia anomala* (1, gemmiparous shoot, with normal, round leaves below; 2, gemmae; 3, cells from leaf-middle; 4, cells from gemmiparous leaf). 5-7. *Marsupella emarginata* (5, sterile shoot, ventral view; 6, fertile shoot, dorsal view (a, capsule; b, seta; c, perianth; d, bracts); 7, leaf). 8, 9. *Jungermannia lanceolata* (8, cells of leaf-middle; 9, fertile plant, showing concave male bracts below perianth).

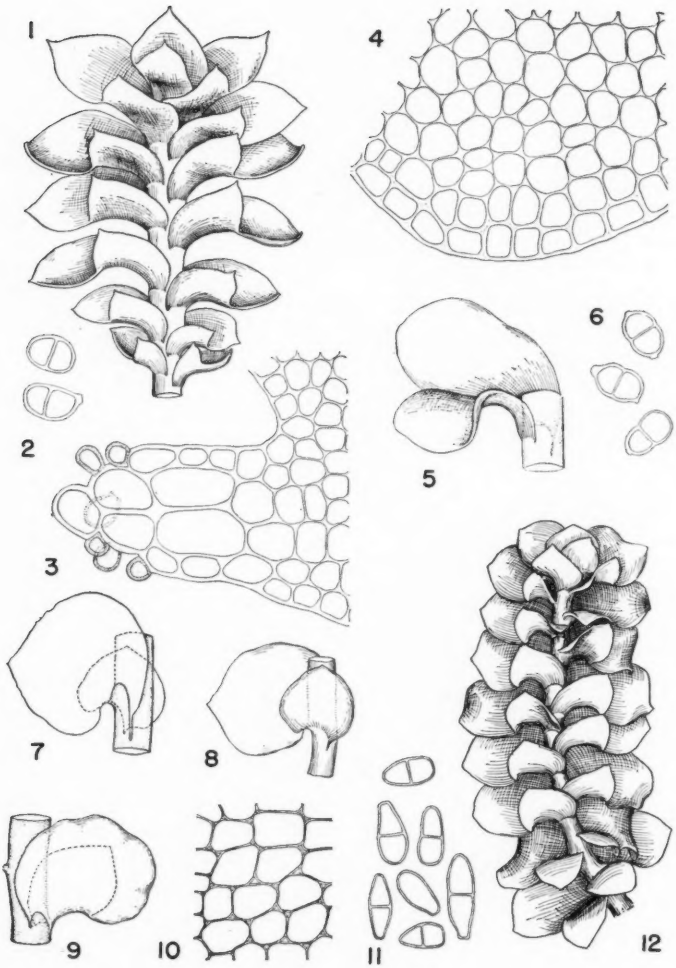

Plate 12. Figs. 1-12.—1-3. *Scapania* (*Scapaniella*) *glaucocephala* (1, large sterile shoot free of gemmae; 2, gemmae; 3, cells of leaf-apex of gemmiparous leaf). 4-6. *Scapania* (*Buchiella*) *cuspiduligera* (4, dorsal leaf apex; 5, leaf, dorsal view; 6, gemmae). 7, 8. *Scapania paludicola* (7, leaf, ventral view; 8, leaf, dorsal view). 9-12. *Scapania irrigua* (9, leaf, ventral view; 10, cells of leaf-middle; 11, gemmae; 12, sterile shoot).

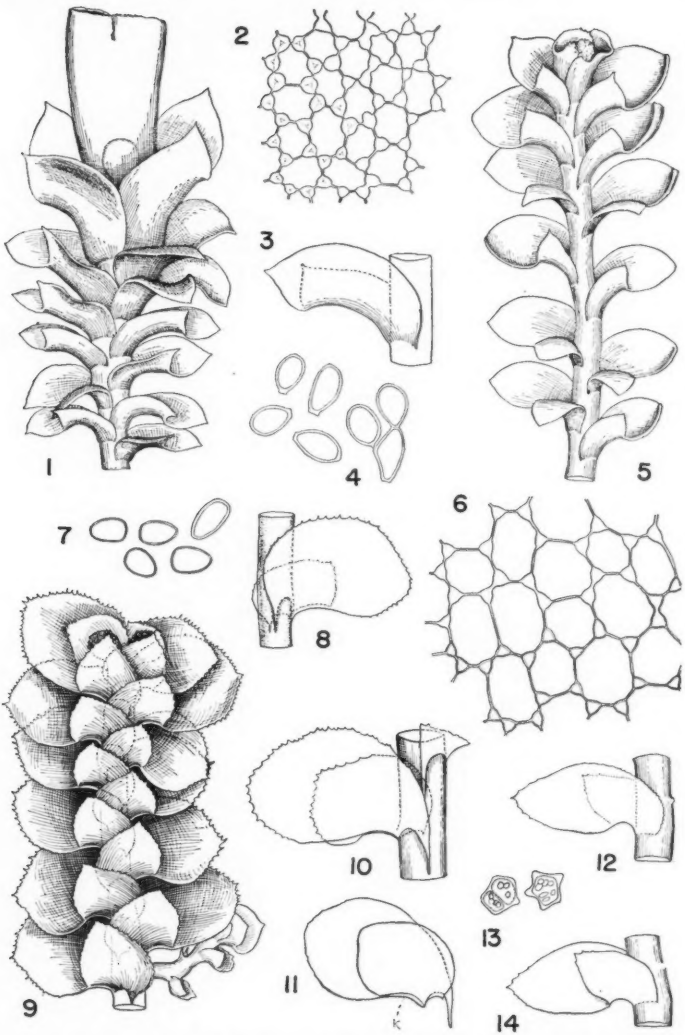

Plate 13. Figs. 1-14.—1-4. *Scapania apiculata* (1, fertile shoot; 2, cells of leaf-middle; 3, leaf, ventral view, showing lack of decurrence; 4, gemmae). 5, 6. *Scapania mucronata* (5, sterile gemmiparous shoot; 6, cells of leaf-middle). 7-9. *Scapania nemorosa* (7, gemmae; 8, leaf, ventral view; 9, gemmiparous shoot). 10, 11. *Scapania undulata* (10, leaf, ventral view; 11, leaf, dorsal view). 12-14. *Diplophyllum apiculatum* (12, leaf, ventral view; 13, gemmae; 14, leaf, dorsal view).

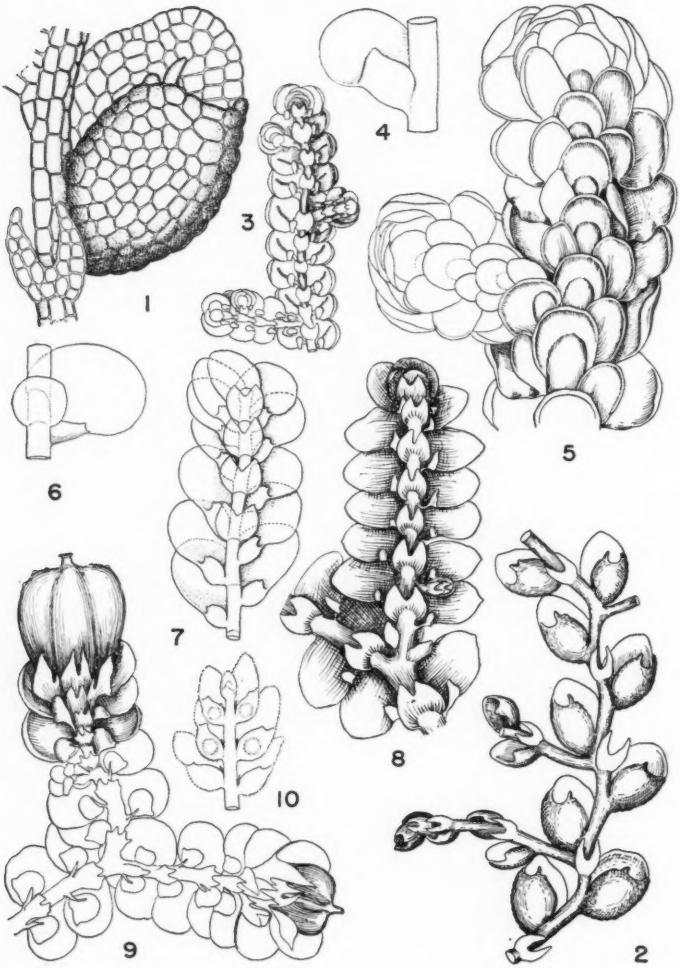

Plate 14. Figs. 1-10.—1, 2. *Microlejeunea ulicina* (1, part of shoot, ventral view; 2, plant, ventral view). 3. *Frullania asagrayana* (sterile shoot). 4. *Radula complanata* (leaf, ventral view, showing absence of rhizoids from stem and absence of underleaf). 5. *Porella platyphylloidea* (shoot, ventral view). 6. *Leucolejeuna clypeata* (leaf and underleaf). 7. *Lejeunea cavifolia* (shoot, ventral view). 8. *Jubula pennsylvanica* (shoot, ventral view). 9. *Frullania eboracensis* (fertile shoot, ventral view). 10. *Cololejeunea biddlecomiae* (apex of male shoot).

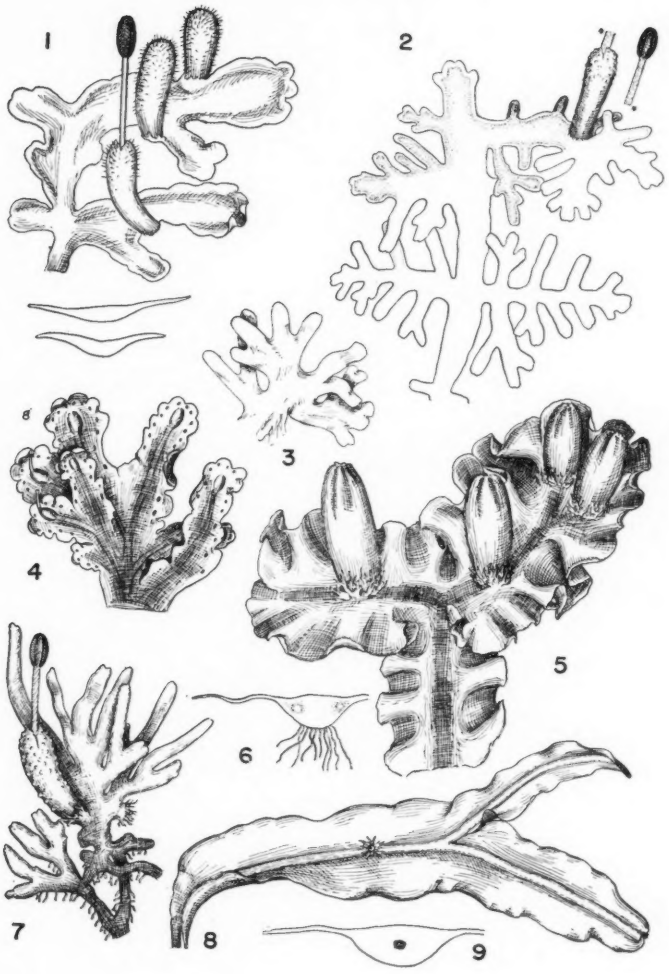

Plate 15. Figs. 1-9.—1. *Riccardia pinguis* (fertile shoot; with two cross-sections of the thallus below it). 2. *Riccardia multifida* (fertile plant). 3. *Riccardia latifrons* (part of sterile plant). 4. *Blasia pusilla* (gemmiparous part of plant). 5, 6. *Moerkia flotowiana* (5, plant; 6, cross-section of thallus, the lateral vestigial conducting strands indicated). 7. *Riccardia palmata* (female plant). 8, 9. *Pallavicinia lyellii* (8, plant with inflorescence, only the outer ring developed yet; 9, cross-section of thallus).

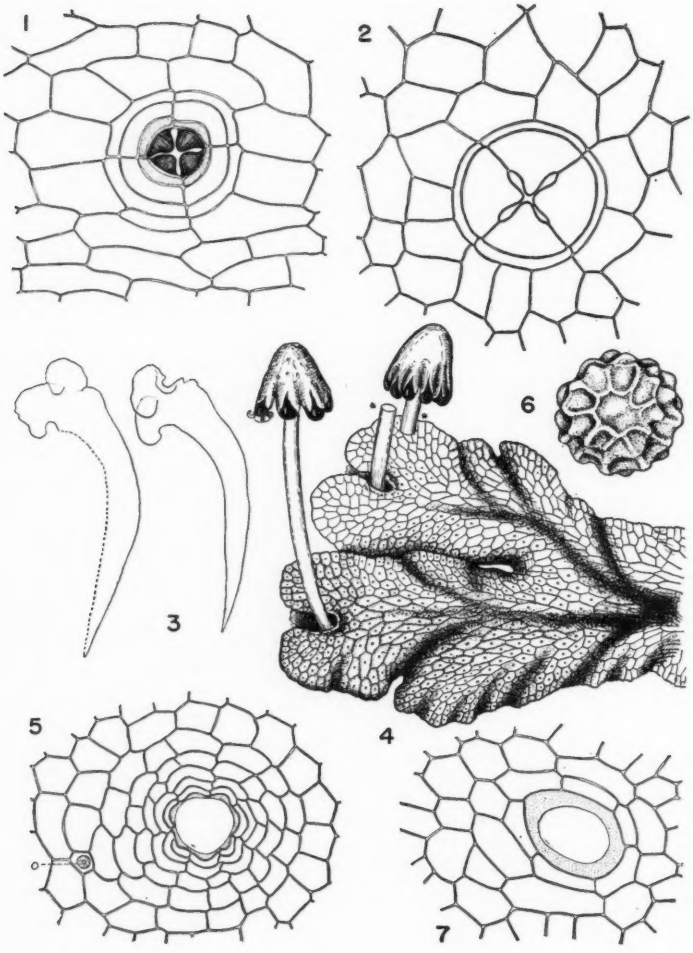

Plate 16. Figs. 1-7.—1, 2. *Preissia commutata* (1, dorsal view of old part of thallus, showing pore, with projecting lower circle of cells of pore cross-hatched; 2, same, ventral view). 3-5. *Conocephalum conicum* (3, ventral scales; 4, fertile plant with mature capsules; 5, pore and oil cell, *o*). 6, 7. *Mannia rupestris* (6, spore; 7, pore of thallus).

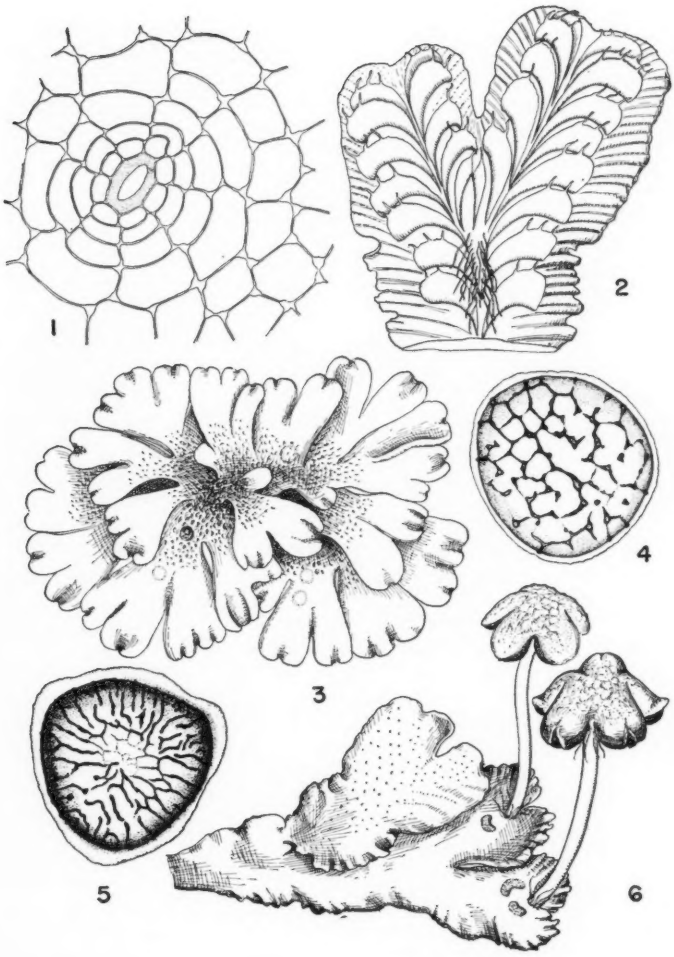

Plate 17. Figs. 1-6.—1, 2, 6. *Reboulia hemisphaerica* (1, large pore of mesodermous form; 2, ventral view of thallus; 6, fertile plant). 3, 4. *Riccia crystallina* (3, fertile thallus; 4, spore). 5. *Riccia frostii* (spore).

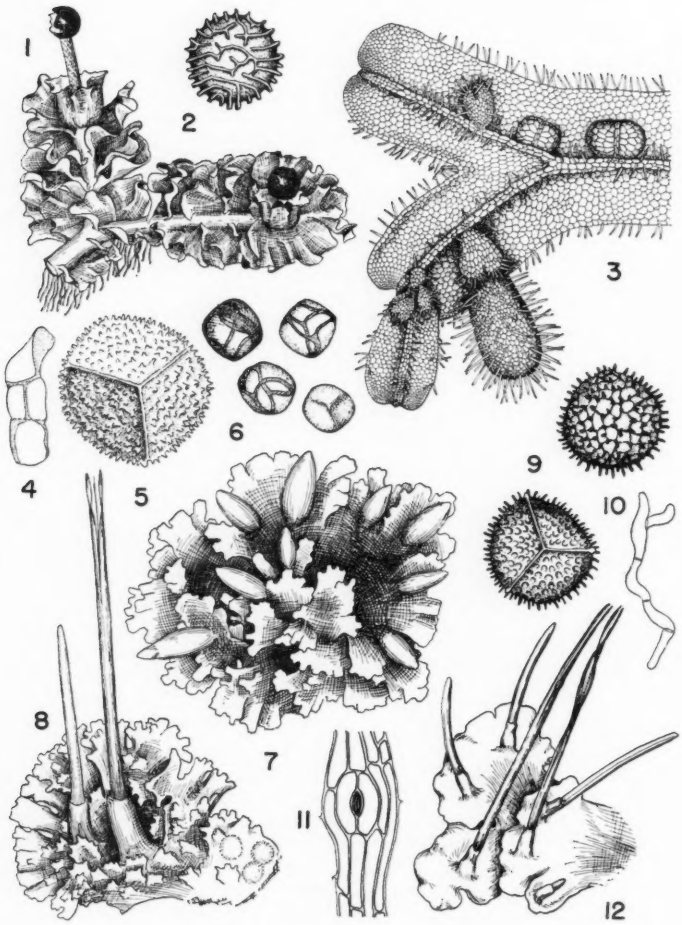

Plate 18. Figs. 1-12.—1, 2. *Fossombronia wondraczekii* (1, fertile plant; 2, spore). 3. *Metzgeria conjugata* (ventral view of fertile plant, with calyptra, archegonial branches, and antheridial branches). 4, 5. *Anthoceros macounii* (4, large elater; 5, spore, inner view, showing muriculate surface). 6, 7. *Notothylas orbicularis* (6, three pseudoelaters and one spore; 7, fertile plant). 8-10. *Anthoceros crispulus* (8, fertile plant; 9, spores, inner and outer views; 10, pseudoelater). 11, 12. *Anthoceros laevis* (11, stoma of sporophyte; 12, part of fertile plant).

APPENDIX[79]

CEPHALOZIA LAMMERSIANA (Hüben.) Spruce

WYOMING CO.: On moist steep shale talus and associated narrow ledges of bed-rock, gorge of Genesee River, Letchworth Park, July 29, 1949, *R. M. & O. M. Schuster;* same data, but on shaded, wet, decaying log.

The present collection is critical, since it stands nearly midway between *lammersiana* and *bicuspidata.* The perianths are uniformly on long, leafy shoots, and the bracts are 3/5-2/3 bilobed into entire, lanceolate-triangular lobes, while the leaves are 12-14 cells wide, much as in typical *lammersiana.* Flagellae, furthermore, are rare and only a single one could be demonstrated. The leaf-cells are merely 32-36, rarely 38 μ wide x 38-56 μ long, hence scarcely large enough to warrant placing the species in *lammersiana.* The plants on the talus slope occurred under conditions typical for the *Lophozia-Scapania* Associule, together with *L. alpestris, Sc. nemorosa* and *curta, Gymnocolea inflata* (var. *heterostipa*), and *Plectocolea crenuliformis.* The second collection, from a nearby decaying log, occurred together with *Lophocolea heterophylla.* A third patch of plants was also found on a loamy bank nearby, under more xeric conditions, together with *P. crenulata* and *C. media* (p. 539).

CEPHALOZIELLA BYSSACEA (Roth) Warnst.

STEUBEN CO.: On thin soil of talus, over steep, rocky slope, circa 4 miles s.e. of Haskinville, July 29, 1949, *Schuster.*

The plants of the present collection occurred much under the same conditions as cited for the species from Tompkins, Chemung and Ontario counties: together with *Lophozia barbata, Tritomaria exsectiformis,* and *Scapania mucronata.*

The collection is of strongly gemmiparous male plants. It is cited since it represents one more link in the accumulating evidence to show that *C. "papillosa"* is not a good species (much less a "subgenus", as Frye and Clark treat it). Some 50 individual shoots were studied, all but 3-4 of which had entire lobes on non-gemmiparous leaves, and had no trace of conical outgrowths of the backs of the leaves. On a few plants isolated leaf-lobes showed marginal teeth, formed by projecting cells; on two plants such marginal teeth were correlated with the presence of a few conical cellular outgrowths of the backs of the leaves (typical for *"papillosa"*). It would appear to the writer that *byssacea* potentially has the ability to produce such dentate leaf-lobes and conical outgrowths of the backs of the leaves, when ecological conditions (probably greater intermittency of moisture) are "conducive." This suggests that *"papillosa"* represents possibly a modification, rather than a "subgenus" of its own (see pp. 547-549).

LOPHOZIA (BARBILOPHOZIA) BARBATA (Schmid.) Dumort.

STEUBEN CO.: About 4 miles s.e. of Haskinville, on road to Avoca, July 29, 1949, *Schuster.*

The plants here under conditions characteristic of the *Lophozia-Scapania*

79 The following important collections, made during the summer of 1949, were worked up after receipt of page galley. The page in the main portion of the paper to which these references pertain is indicated in each case.

Associule, occurring with *Sc. mucronata* and *Tritomaria exsectiformis* (p. 565).

LOPHOZIA (LEIOCOLEA) BADENSIS (Gottsche) Schiffn.

WYOMING CO.: On steep, vertical gorge walls of Genesee River, below "The Flume," Letchworth State Park, July 29, 1949, *R. M. & O. M. Schuster.*

The plants were more abundant here than anywhere else I have seen them in New York, and bore capsules. Together with *Gymnostomum curvirostrum* they formed the matrix in which the rare boreal *Saxifraga aizoides* underwent ecesis (p. 53).

LOPHOZIA (DILOPHOZIA) ALPESTRIS (Schleich.) Evs.

WYOMING CO.: Letchworth State Park, in gorge of Genesee River, about ¼ mile below "The Flume," July 29, 1949, *R. M. & O. M. Schuster.*

This species occurs frequently on vertical rock-walls and over ledges and boulders on cold, shaded cliffs in the Coniferous Forest Region, northward well into the Tundra. As far as I am aware, it has not been previously reported from the Deciduous Forest Region. Its occurrence this far south is surprising, and it is to be regarded fully as much as a "glacial relic" as is the angiosperm, *Saxifraga aizoides*, which occurs on the gorge walls only a few hundred yards upstream. At the above station it occurred over loose, disintegrating shale talus, and on the associated outcrops of undisintegrated rock, especially at points kept moist by seepage. It occurred here with *Cephalozia lammersiana, Scapania nemorosa* and *curta, Gymnocolea inflata heterostipa,* and *Plectocolea crenuliformis,* i.e., with other members of the "calciphobe" *Lophozia-Scapania* Associule, under conditions grading into the *Gymnocolea-Cephalozia bicuspidata* facies (see p. 664).

In the key to species of *Lophozia* (pp. 562-564) it keys to Couplet 16, but no further. It agrees with *L. longidens* in the development of conspicuous reddish-brown gemmae masses; in this feature it differs at once from the *ventricosa-porphyroleuca* complex. In most other features (broad leaves, almost as in Plate 8, fig. 10; decumbent growth; perianth-mouth with very short teeth at most 1 cell long) the species differs obviously from *longidens*, and agrees with the *ventricosa-porphyroleuca* complex. Unlike all three of these species, the leaves are almost circular, bilobed by a lunate sinus for 1/6-1/4 their length, and are more or less strongly concave, often saucer-shaped. Furthermore, the cells of the leaf-lobes are smaller, averaging only 18-21 μ, and the cell-walls and trigones tend to be deeply reddish-brown pigmented, especially on exposed plants (consequently the entire patch of plants usually show a bright reddish-brown to fuscous-brown pigmentation, quite unlike our other species of *Dilophozia*).

Superficially the species might be confused with *L. bicrenata* or *excisa,* because of the orbicular leaves and pigmented gemmae. The thin-walled leaf-cells, with obvious trigones separate the species at once from both *bicrenata* and *excisa*. The species is furthermore dioecious, unlike the latter (p. 568).

LOPHOZIA (DILOPHOZIA) VENTRICOSA (Dicks.) Dumort.

STEUBEN CO.: About 1 mile s.e. of Haskinville, on road to Avoca, July 29, *R. M. & O. M. Schuster;* on exposed, north-facing ledges, together with *Tritomaria exsectiformis, Scapania nemorosa, Ptilidium pulcherrimum.*

Occurring as a member of the *Lophozia-Scapania Associule* (the "calciphobe" *L. ventricosa* facies) under conditions approaching the xeric extreme, hence the consociation of *P. pulcherrimum* (p. 568).

LOPHOZIA (DILOPHOZIA) EXCISA (Dicks.) Dumort.

TOMPKINS CO.: South Hill Marsh, among *L. bicrenata, Schuster.*

The plants of the above collection were overlooked for several years, because they were virtually identical in form with the locally more common *L. bicrenata,* and showed some reddish-brown pigmentation like the latter. The crenulate perianth-mouth and thin-walled cells contrast strongly with *L. bicrenata,* however. Occurring here as a member of the *Lophozia bicrenata-Cephaloziella* Associule (p. 570, 660).

LOPHOZIA (MASSULA) MILDEANA (Gottsche) Schiffn.

CHENANGO CO.: Plymouth Pond, over wet peaty log at peaty edge of pond, S. Plymouth, *Schuster & Winne* (p. 571).

TRITOMARIA EXSECTIFORMIS (Breidl.) Schiffn.

STEUBEN CO.: About 1 mile s.e. of Haskinville, July 29, 1949, *R. M. & O. M. Schuster;* on exposed, north-facing ledges, over thin soil and in crevices, together with *Lophozia ventricosa* and *Scapania nemorosa,* i.e., as a member of the *Lophozia-Scapania* Associule (the "calciphobe" *Lophozia ventricosa facies,* see p. 662, 664). Also on n.w. facing ledges, 4 miles s.e. of Haskinville, with *L. barbata* and *Sc. mucronata,* under somewhat subcalcareous conditions (p. 574).

GYMNOCOLEA INFLATA var. HETEROSTIPA (Carr. & Spr.) Lindb.

WYOMING CO.: Gorge of Genesee River at Letchworth Park, with *Lophozia alpestris, Sc. nemorosa, C. lammersiana, Plectocolea crenuliformis,* over rather exposed shale talus and associated rock-outcrops, *R. M. & O. M. Schuster.*

See ecological notes under *L. alpestris.*

The plants of the present collection are quite atypical for *G. inflata.* The large majority of branches are postical in origin; many of the plants show acute to merely obtuse leaf-lobes (thus approaching the entirely saxicolous *G. acutiloba*); the leaves are often rather concave and imbricate, and the plants are relatively small in sze. The latter is perhaps due to heterothallism, since the plants are all male, and show the spicate, elongate androecia of the species (often, however, with as many as 7-12 pairs of bracts). It is questionable how distinct the var. *heterostipa* is; it differs from typical *inflata* largely in the numerous postical, and relatively few lateral branches. In the many postical branches, the var. *heterostipa* may give rise to confusion with *Cladopodiella;* it differs from the latter at once in lacking stolons, virtually lacking underleaves, and in the smaller leaf-cells (nearly quadrate in the lobes and mostly less than 28 μ long; in *Cladopodiella* 35 μ-45 μ or even larger).

In the often subacute leaf-lobes some plants are similar to the questionable *G. acutiloba.* Macvicar (1926) has commented on the difficulty of keeping these two species apart, and notes that the var. *heterostipa* appears to connect them. This variety has been reported once before from North America (Washington, *Foster*) (p. 577).

PLECTOCOLEA CRENULATA (Sm.) Evans

WYOMING CO.: Letchworth Park, *R. M. & O. M. Schuster.*

Two collections are at hand, one from a relatively xeric site on exposed soil along a path through Oak-Hickory woods at the crest of the ravine, here with *Cephalozia media,* the other from atypical surroundings: associated with *Lophozia alpestris, Cephalozia lammersiana* and *Scapania nemorosa,* on shale talus (see ecological notes under *L. alpestris*) (p. 582).

PLECTOCOLEA CRENULIFORMIS (Aust.) Mitt.

WYOMING CO.: Gorge of Genesee River, ¼ mile below "The Flume," Letchworth Park, July 29, 1949, *R. M. & O. M. Schuster.* New to New York State.

This species occurs commonly on moist rocks along streams. At the sole station for the species in our area, it occurred on the moist, but rather exposed, shale talus, and over narrow associated ledges of the bed-rock, forming extensive, pure green patches, or growing scattered among other members of the lime-"avoiding" *Lophozia-Scapania* Associule, such as *Scapania nemorosa, Sc. curta, Lophozia alpestris, Gymnocolea inflata* (var. *heterostipa*), and *Cephalozia lammersiana;* it occurred under conditions intermediate between those characterizing the mesic *Lophozia ventricosa* facies and the mesic-hygric *Gymnocolea-Cephalozia bicuspidata* facies (see p. 664).

The species can easily give rise to confusion with two other local forms, *Jungermannia caespiticia* (found in Ontario County under extremely similar conditions) and *Plectocolea crenulata* (occurring sparsely with the above species, under identical conditions, at Letchworth Park). All three species are more or less pure-green to yellow-green, rarely reddish-tinged, all have nearly or quite orbicular leaves on sterile shoots, and all are moderate-sized species (about 1.5-2 mm. wide x 1-2 cm. long); finally, all three occur only on mineral substrates with a high water-retaining capacity, such as clay soils over talus.

P. crenuliformis differs at once from *J. caespiticia* in that the leaf cells have several rather large oil-bodies (in local plants 5-7 per cell near the marginal region, up to 12-16 per cell in median and basal leaf-cells; these oil-bodies in young leaves from 5 x 7 μ to 7 x 12 μ, a few to 9 x 15 μ), and in that the marginal cells of the leaves are rather swollen, turgid, and form a slightly raised border: the rest of the leaf-plane appearing somewhat depressed compared to the margin. This border is rather obscure and best visible with a strong hand-lens or under the binocular microscope, at low powers. The species differs from *P. crenulata* in that the swollen marginal leaf-cells are virtually identical in size with the interior cells of the leaf, and in the larger and more numerous oil-bodies (in *P. crenulata* these are present in only some cells, absent in most of the swollen marginal cells, and where present fill only a small portion of the cell-lumen; they occur mostly 2-3 per cell and vary from 4.5-6 μ in diameter, with the largest 5.5 x 9 μ).

The species differs from both *J. caespiticia* and *P. crenulata* in having distinct trigones in the leaves (often slightly bulging, much as figured for *J. lanceolata,* Pl. 11, fig. 8); in this it approaches *P. hyalina;* it also differs from

them in that the bracts are fused with the perianth for 1/4 or more the length of the perianth (in *caespiticia* the bracts are quite free; in *crenulata* they are nearly or quite free). In the connate bracts and perianth *P. crenuliformis* again approaches *P. hyalina*. The rhizoids in the present species are generally reddish or purplish (at times only lightly pigmented, as in the present collection), much as in *P. hyalina*, but quite unlike *J. caespiticia* and *P. crenulata*.

Although approaching *P. hyalina* in many characters, the present species differs from it in the border of turgid, swollen marginal leaf-cells; in the non-undulate female bracts (and subtending leaves); and in that the perianth is nearly or quite included within the bracts, extending beyond them for at most 1/4 its length (in *hyalina* about 1/2 emergent). *P. crenuliformis* may also have the cuticle slightly, delicately verruculose, as in the present collection; in *hyalina* it is smooth. In the present collection the several old, weathered perianths found were fused with the bracts for 2/5-1/2 their length—slightly more than is normal for *hyalina*. In having up to 12, occasionally 16 oil-bodies per cell *P. crenuliformis* also differs from *hyalina* (2-4 oil-bodies per cell, *fide* K. Müller, 1939); in both species they are ovoid or elliptical and attain about the same maximum size (6 x 18 μ) (p. 582).

The leafy liverworts with nearly or quite orbicular leaves on sterile, non-gemmiparous portions of shoots, are often extremely difficult to separate on the basis of sterile plants. For determination of such plants the generic key (starting with couplet 19, p. 522) will often prove inadequate. The following supplemental key, using largely cytological features is more reliable for living material. (In plants that have been dry for no more than 1 year the oil-bodies often persist in some or many cells; in such cases they can be determined using this key):

1. Rhizoids scattered all over postical stem-surface 2
2. Stolons normally absent; gemmae never on erect, reduced-leaved shoots 3
3. Oil-bodies smooth or appearing faintly granular: not looking like a cluster of grapes; gemmae never present on apices of leaves; median leaf-cells less than 45 μ, no obvious underleaves 4
4. Oil-bodies occurring 2-4 or more per cell, less than 6 x 18 μ in size; median leaf-cells less than 38 μ (or with distinct trigones); gemmae absent 5
5. Marginal leaf-cells 2-3 x the inner leaf-cells in size, forming a very obvious, swollen border; oil-bodies small, mostly 2-3 per cell, mostly 5 x 7 μ or smaller, obscuring less than 1/3 the cell-area; cells lacking trigones, but often more or less equally thick-walled ..... *Plectocolea crenulata*
5. Marginal leaf-cells about equal in size to inner cells, forming a slight or no border; cells all with distinct (even if minute) trigones 6
6. The larger oil-bodies of median cells of leaf 5-7 x 12 μ to 9 x 15 μ, obscuring most or all of cell-surface; rhizoids often reddish or purplish .. 7
7. Each cell with 2-3, rarely 4 oil-bodies; cuticle smooth; marginal leaf-cells not swollen, not forming a distinct elevated border ..... *Plectocolea hyalina*
7. Each cell (at least of the actively growing younger leaves) with 5-7, occasionally 12-16 oil-bodies, nearly filling it; cuticle often faintly verruculose; marginal leaf-cells obscurely swollen, turgid, somewhat elevated above rest of leaf-surface ..... *Plectocolea crenuliformis*
6. Oil-bodies 4-5 up to 5 x 9 μ, 7-12 per cell, never more than twice as

long as wide, obscuring half or less of cell-lumen; rhizoids colorless ..... *Jamesoniella autumnalis*

4. Oil-bodies occurring merely 1 per cell, 8-10 x 16-20 μ large; median leaf-cells mostly 38-45 μ, extremely thin-walled, lacking trigones; often with gemmae produced on the inside of large, swollen, brownish globose terminal "heads" at the stem-apices; marginal leaf-cells not swollen ..... *Jungermannia caespiticia*

3. Oil-bodies composed of a few globular, large, homogeneous oil-globules (therefore appearing like small clusters of grapes), up to 8 x 14-18 μ, up to 10-20 per cell; gemmae at apices of upper, narrowed, lanceolate leaves; median leaf-cells 45-55 μ, with bulging trigones ..... *Mylia anomala*

2. Stolons numerous; gemmae present at apices of erect, reduced-leaved, flagelliform shoots; oil-bodies 2-3 per cell, up to 7 x 14 μ; cells with bulging trigones ..... *Odontoschisma denudatum*

1. Rhizoids absent except at bases of some or all underleaves; leaf-cells thin-walled, lacking trigones; oil-bodies of grape-cluster type, several per cell .....see *Chiloscyphus* sp.

SCAPANIA MUCRONATA Buch

STEUBEN CO.: Over thin clayey soil on narrow ledges and steep talus slope of cliff 4 miles s.e. of Haskinville, July 29, 1949, *Schuster.*

Occurring with *L. barbata, T. exsectiformis* (see *L. barbata* for ecological notes).

The American material of this species, as noted by Evans (1936, Rhodora 38: 77-90) tends to have the ventral leaf-lobes obtuse, occasionally even rounded, with the apex often indicated by merely a single projecting cell—thus belying the species name. Whether this material is genetically identical or similar to the European species is somewhat questionable. The writer therefore has carefully studied the cytological features of the species, since American *mucronata,* in the obtuse ventral lobes, very closely approaches the rare *Sc. buchii* K. Müll. (= *lingulata* Buch.). In the above collection the oil-bodies of the marginal 3-5 rows of cells occurred mostly 3-6, rarely 7-8 per cell, and were present in all uninjured cells; they varied from circular and 3.6-4.0 μ to ovoid and 4-5.4 x 6-7 μ. In the leaf-middle the cells had from 4-6, occasionally 7-8 oil-bodies (as in the marginal cells); these averaged slightly larger, from 4 x 5.5 to 5.5 x 7.5 μ, with a few as large as 5 x 9 μ. In the leaf-bases the oil-bodies were similar in size to those of the leaf-middle, but occurred mostly 7-12 per cell.

Buch (1928) states that in European *mucronata* there are 2-6 oil-bodies per cell in the marginal and median cells, with up to 8 oil-bodies per cell in the basal leaf-cells. He describes *buchii* (*lingulata*) as having 6-12 oil-bodies per cell in the upper (and marginal) leaf-cells, with the basal cells containing up to 20 oil-bodies.

The plants from the local area, therefore, are somewhat intermediate in the number of oil-bodies per cell, but most closely approach *Sc. mucronata.* The marginal leaf-cells also average only 15-18 μ (typical for *mucronata;* in *buchii* 20-26 μ). Numerous other collections of living *mucronata* studied from New York to Michigan, Wisconsin, and Minnesota, all show the same tendency for the development of obtuse ventral lobes and slightly more numerous oil-bodies. It is therefore apparent that nearctic *mucronata,* with its obtuse to subacute ventral lobes (Plate 13, fig. 5) and more numerous oil-

bodies approaches *buchii*. However, *buchii* has decidely more numerous oil-bodies, and larger marginal leaf-cells, as well as slightly larger gemmae. In *mucronata* Buch describes the gemmae as 8-14 x 16-29 μ; in the present collection they are 10-13 x 20-27 μ when mature (in *buchii* the larger are up to 12 x 35 μ).

All of the local material of *mucronata* seen (including the present collection), represents a modificatio *leptoderma-viridis*, e.g., has slight and merely concave trigones and no secondary pigmentation. Such plants with small trigones are very difficultly separable from *Sc. curta*. The latter normally develops a border of equally thick-walled marginal leaf-cells (always lacking in *mucronata* and *buchii*); in the mod. *leptoderma-viridis* this marginal border is not or scarcely indicated, and the plants have the cells almost identical in form with those of *mucronata*. The cell-size and facies of the two species are also extremely similar. In extreme cases, therefore, one has to depend on the oil-bodies in order to affect a separation between *mucronata* and *curta* (those in *curta* being smaller and lying only 2-4 in each cell) (p. 596).

SCAPANIA CURTA (Mart.) Dumort.

Extremely rare locally. WYOMING CO.: Gorge of Genesee River, below "The Flume," Letchworth Park, on moist, steep shale talus and shale ledges, July 29, 1949, *Schuster;* scattered among *Cephalozia lammersiana, Lophozia alpestris, Scapania nemorosa,* etc. New to New York; the southernmost verified station in North America.

The present collection consists of a relatively few gemmiparous plants. These can be referred here definitely because of the presence of the following diagnostic characters: color nearly pale green throughout, but stems somewhat purplish and postical leaf-bases vineous-red pigmented, as well as a few dorsal lobes; postical leaf-bases with the border of equally thick-walled marginal cells very obvious, while the rest of the leaf with 1-2 marginal rows of cells slightly evenly thick-walled; interior leaf-cells with concave trigones; oil-bodies absent from many cells (especially near leaf-bases, in the pigmented region): where present merely 2-4 per cell, and only 4-5 μ in diameter and almost constantly spherical; the diameter of the oil-bodies averaging less than 1/6-1/8 the length of the containing cells and the lumen obscured for less than 0.25 its area.

Except for these differences the species agrees very closely with *Sc. mucronata* in the vegetative features; it keys to it in the key on p. 594: like the latter it shows narrow ventral leaf-lobes, is small in size (mostly 1.5-2 mm. wide), has yellowish-green 2-celled gemmae, and quite non-decurrent leaf-bases. In *Sc. mucronata* any secondary pigmentation that is developed is brownish, never reddish or purple, and the leaf-cells are all equally collenchymatous, with the marginal cells never thick-walled. Fertile plants of *curta* have the perianth-mouth with the teeth only 1-3 cells long; in *mucronata* they form a fringe, with the individual laciniae or ciliate lobes 5-10 cells long. The greenish gemmae (in the present collection) were 11-12 x 18-23 μ, and agree closely with those of *mucronata*.

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Observations of the Life Cycle and Larval Development of Paruterina candelabraria (Goeze, 1782) (Cestoda: Dilepididae)[1]

Robert Rausch[2]

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Paruterina candelabraria (Goeze, 1782) is parasitic in owls in Europe and North America, and appears to be the most frequently encountered cestode occurring in strigiform birds (Wolffhügel, 1900; Rausch, 1948). It is the purpose of this paper to present observations on the larval development and life cycle of *P. candelabraria*. Apparently nothing is known concerning the life cycles of cestodes of the genus *Paruterina* Fuhrmann, 1906, most of which occur in passeriform birds.

During the spring of 1948, the author succeeded in obtaining the larvae of *Paruterina candelabraria* experimentally in three laboratory mice (Rausch, 1948). Extremely heavy liver infections were observed when the mice were killed and examined a month after the infection attempt (plate I, fig. 1). Part of the infected livers were fed to a captive great horned owl, *Bubo v. virginianus* (Gmelin), but no cestodes were recovered when the bird was autopsied a month later. Attempts to infect a grey squirrel, *Sciurus carolinensis leucotis* Gapper, at the same time were unsuccessful.

The study of the infected mouse-liver sections disclosed that the larvae were cysticercoids (plate II, figs. 1 and 2)—a larval type of unusual occurrence in mammalian tissue. In order to make possible additional observations, an attempt was made to obtain material that would allow the infection of a larger number of experimental animals. We were particularly interested in attempting the infection of certain native mice which, in the region where this work was done, form the bulk of the food of the larger owl species.

Through the generous cooperation of Mr. Stephen H. Richards, Wildlife Biologist with the Wisconsin Conservation Department, a second naturally-infected owl was obtained during the fall of 1948, and the gravid segments from 4 worms were used to infect experimental animals.

The mammals used for this work were anesthetized and given one gravid segment each by means of a stomach tube. Thirty-six laboratory mice, from 17 to 20 days old, were infected, as were hamsters, chipmunks, *Tamias striatus* L. ssp., white-footed mice, *Peromyscus maniculatus bairdii* Hoy and Kennicott, and a single meadow vole, *Microtus p. pennsylvanicus* Ord. It was at first the intention to kill the white mice every second day, in order to observe

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2 Now with the U. S. Public Health Service, P. O. Box 960, Anchorage, Alaska.

larval development; however, this development took place with such rapidity that, after the first few days, mice were killed daily.

Four mice, killed and examined for infection on the 21st day, were found heavily infected, and were fed to a captive great horned owl. The owl was

PLATE I

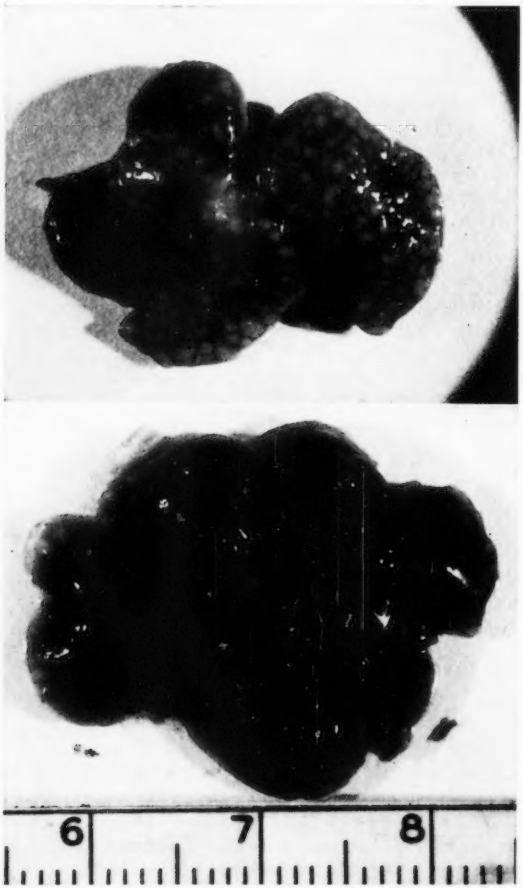

Fig. 1.—Liver of laboratory mouse showing severe infection with *Paruterina candelabraria* larvae (upper). Photograph taken 30 days after experimental infection.

Fig. 2.—Liver of laboratory mouse showing moderate infection with *Paruterina candelabraria* larvae. Photograph taken 30 days after experimental infection.

killed on the 7th day after this feeding, and more than 60 specimens of *Paruterina candelabraria* were removed from the small intestine. These worms were immature, and measured about 12 mm. in length. The owl used for this experiment had been a captive for more than 6 months, and during this time had been given only a prepared fox food. There was no opportunity for its becoming infected with the species of cestode with which we are concerned.

As the mice were killed daily, their livers (the only part of the body infected by larvae of *Paruterina candelabraria*) were fixed in either alcohol-acetic acid-formalin solution, or in 10 per cent formalin. In a few cases special fixatives were used. The sections were routinely stained with Crossman's modification of Mallory's triple stain, and special methods were used for the determination of certain specific details. An effort was made to follow the cellular reaction of the host tissue to the larvae during the course of their development.

The experimental animals were infected on September 29, and the first mouse was examined on the second day after infection. The liver of this animal showed no gross changes. The liver of the animal killed on the third day showed numerous small hemorrhages on the surface of the liver. There was considerable congestion, probably as a result of larval migration through the blood vessels of the liver. The larvae were clearly visible on the surface of the liver by the 6th day, when they were seen as white spots measuring from 0.5 to 1.5 mm. in diameter. By the 8th day the larvae were larger and more obvious. Larvae were observed only in the peripheral part of the liver, regardless of the severity of the infection. However, with extremely heavy infections (plate I, fig. 1) the connective tissue capsules surrounding the larvae coalesce, and raised areas on the surface of the liver were commonly seen. Moderate infections had much the same gross appearance as liver infections by the cysticerci of *Cladotaenia* spp. However, they can be microscopically differentiated at the time they are dissected from the host tissue—the cysticerci being readily recognized as such.

Microscopically, considerable hyperemia was seen in the liver of the mouse killed on the second day after infection. In some areas hemorrhage was evident. The liver obtained on the third day showed areas of infiltration by neutrophile and mononuclear cells, and there were scattered peripheral foci of beginning necrosis. By the 6th day peripheral areas of necrosis, surrounded by inflammatory cells in which macrophages were predominant, were much in evidence. Damaged liver cells were seen within the necrotic areas, and small larvae were occasionally observed within the capillaries. The irregular congestion observed at this stage of larval development was perhaps caused by the localization of the larvae, in contrast to the generalized hyperemia seen earlier. Necrosis had become more extensive by the 8th day; neutrophiles were more numerous, and the mononuclear cells had almost disappeared from some areas. By this time the larvae had migrated deeper into the liver tissue, leaving behind them rather extensive areas of necrosis. Little reaction was observed around the parasites, which had migrated inward away from the peripheral areas of necrosis. There was little change in the necrotic areas.

After the 10th day, there was little change around the larvae themselves

PLATE II

Fig. 1.—Photomicrograph, taken 30 days after infection, of liver of laboratory mouse infected with cysticercoids of *Paruterina candelabraria* (upper). This section was made from the same organ shown in plate I, fig. 1. Low power.

Fig. 2.—Photomicrograph, taken 30 days after infection, of a single cysticercoid of *Paruterina candelabraria* in the liver of an experimentally infected laboratory mouse. Typical larval form and macrophages lining connective tissue capsule are shown. Medium power.

except for a gradual proliferation of the connective tissue capsule. The trail of the parasite persisted as an area of fibroblastic infiltration, with some lymphocytes and atrophy of adjacent liver cells. About the 12th day a considerable amount of yellow pigment was observed in the Kupffer cells, particularly in areas near the parasites. The Gmelin Reaction was not obtained for hematoporphyrin or bilirubin, and the test by Turnbull's method for hemosiderin was also negative. By the 18th day the fibrosis around the parasites was rather extensive; polymorphs were numerous and macrophages, with their cytoplasm filled with granules, were abundant within the capsules near the parasites. On the 22nd day foam cells (plate III, fig. 1) were noted near the parasites. These were at first thought to be macrophages which had phagocytized fat, but suitable stains failed to demonstrate any fat. For this information, the livers were frozen-sectioned and stained with Sudan IV by the Lillie method, and also by the osmium tetroxide method. The yellow pigment persisted in the Kupffer cells in the proximity of the larvae. The toluidin blue test for mast cells and the Unna-Pappenheim plasma cell stain both gave negative results.

The connective tissue capsule reached maximum thickness by the 30th day. It averaged about 70 μ in thickness at this time. There seemed to be little or no change in this as late as the end of the second month after infection. At 30 days the capsule, containing the larva, measured about 850 by 550 μ, and the undisturbed larva measured about 700 by 280 μ.

After the 15th day it was noted that macrophages were numerous within the connective tissue capsule surrounding the parasite (plate II, figs. 1 and 2; plate III, fig. 1). These cells persisted in this location for at least 60 days after infection—as long as observations were made. In the mice, however, there was never any invasion of the parasites.

In other mammalian species.—The infection in the hamsters took the same course as that in laboratory mice. That seen in the white-footed mice also did not differ in any appreciable way. The single vole infected died on the second day after infection. The liver of this animal showed congestion comparable to that seen in laboratory mice in the early stages of the infection. Since voles may die rather frequently when kept under laboratory conditions, we do not consider the death of this animal to be connected in any way with the parasite infection. It might be mentioned here that in no case, regardless of severity of infection, was there any recognizable effect on the physical condition of the infected animals.

Only two chipmunks were infected, so observations on this species are limited. However, when a heavily-infected animal was examined on the 21st day, the host tissue-reaction appeared to be much more severe than any seen in the other mammals. Although the larvae had migrated away from the peripheral areas of necrosis, they were closely surrounded by the tissue reaction (plate III, fig. 2). Giant cells (plate III, fig. 2), unobserved in the other mammals, were common. The question arises as to whether the larvae might not be destroyed by the tissue reaction of the chipmunk. As discussed further below, it is improbable that the chipmunk would serve as a suitable intermediate host for this owl cestode.

PLATE III

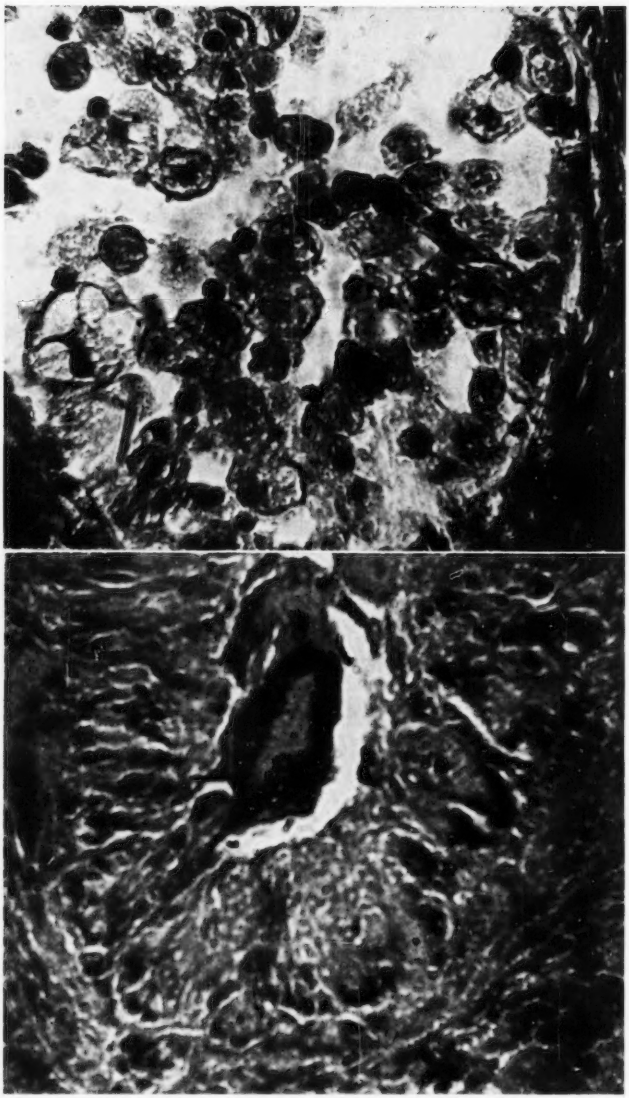

Fig. 1.—Foam-cell macrophages within fibrous connective tissue capsule surrounding larvae (upper). High power.

Fig. 2.—Tissue reaction of chipmunk to larvae of *Paruterina candelabraria*. Necrotic tissue is abundant, and a multinucleated giant cell is shown near top of section. Medium power.

DISCUSSION

An effort was made to compare the tissue reaction of mammals infected with the larvae of *Paruterina candelabraria* with that seen in similar infections by other cestode species. It might be of some value to mention these briefly.

Taenia taeniaeformis larvae.—An early infection by the strobilocercus of this cestode in the liver of a laboratory mouse was studied. A very thick cyst wall composed of fibrous connective tissue was seen. Within the capsule, and lining its wall, were numerous lymphocytes and macrophages. Some of the latter contained a yellow pigment within their cytoplasm, and others contained a granular material. There appeared to be considerable pressure atrophy of the liver cells adjacent to the capsule surrounding the parasite. The surrounding tissue also contained a considerable amount of yellow pigment, within the cytopasm of the Kupffer cells.

We did not examine histologically any infections by this larval cestode in voles, but some observations were made on an old infection in the liver of a muskrat, *Ondatra z. zibethica* L. A rather thick layer of calcium deposit was seen around the parasite, and surrounding this was a layer of fibrous connective tissue. Outside the connective tissue capsule were seen early deposits of calcium. The adjacent liver tissue was necrotic. A yellow pigment was abundant in the Kupffer cells, in the damaged as well as in the adjacent normal areas. Foam cells were not observed. Athough in some areas the calcium deposits were in direct contact with the cestode, the latter showed no apparent sign of invasion or damage.

Unidentified cestode larvae.—Cestode larvae, thought first to be *Taenia* sp., were taken from the liver of a snowshoe hare, *Lepus americanus* Erxleben, collected in central Manitoba. Although we were unable to assign these larvae to genus, it seems of value to discuss here the reaction brought about by their invasion of the liver tissue of the hare. Large areas of necrosis, surrounded by lymphocytes and fibrous connective tissue, were numerous. In some lesions, possibly earlier ones, giant cells, macrophages, and polymorphonuclear leucocytes were seen. Pigment was abundant in the Kupffer cells near the necrotic lesions. Chronic passive hyperemia was noted. The liver sinusoids in areas adjoining the recently-invaded areas were filled with macrophages and polymorphonuclear leucocytes. Some eosinophiles were present. No foam cells were seen.

Cladotaenia sp.—During November, 1948, at Madison, Wisconsin, an adult vole infected with 10 cysticerci of *Cladotaenia* sp. was collected. The cysticerci were closely encapsulated by fibrous connective tissue. There was some atrophy of the liver cells, and fibroblasts closely surrounded the parasites. There was a moderate infiltration of lymphocytes around the fibroblastic layers. Calcium was deposited around the greater part of each parasite, and cells were seen entrapped within the calcium. The Kupffer cells throughout the liver were filled with a brown, granular pigment, but it was most abundant in the areas surrounding the parasites. There was a chronic passive congestion, and considerable vacuolation of the liver-cell cytoplasm around the parasites.

It is apparent from the foregoing that the tissue reaction to the invasion by the cysticercoids of *Paruterina candelabraria* does not appear to differ significantly from reactions seen in other host species invaded by larval cestodes of other genera.

Certain of the native North American mice (Cricetidae) form a very considerable part of the diet of owls. The house mouse, not a native form, is also preyed upon. It is interesting that a natural infection by *Paruterina candelabraria* has never been reported from rodent intermediate hosts. The author has examined to date a total of 744 specimens of the common meadow vole, and 240 specimens of white-footed mice, all from the North Central States region, and a considerable number of similar rodents from other regions as well. In the North Central States, about 6 per cent of the large owls (*Strix* and *Bubo*) harbour *P. candelabraria* in the small intestine (Rausch, 1948). Although the distribution of this larval cestode in the liver of the intermediate host appears to be such that they would be easily seen, we have failed to detect a single natural infection.

It might be of value to compare incidence of infection of another cestode parasitic in raptors. In the same region (North Central States) *Cladotaenia* spp., the common cestodes of hawks, are often seen as cysticerci in the liver of voles. According to our records, about 16 per cent of the large hawks (*Buteo*) harbour this cestode, and its larvae are found in 3 per cent of the voles. There should be little difference in the detectability of the two species of larvae, since both are situated in the host liver, and they are of similar size. However, many factors are involved, such as relative densities of definitive and intermediate hosts, habitat differences, and the like.

It is almost certain, from indirect evidence, that insects act as the intermediate hosts for cestodes of this genus found in passeriform birds. We were unable to infect beetles (*Tenebrio*) with *Paruterina candelabraria*, but further experiments of this type might be of interest. Certain owl species feed to a large degree upon insects.

It is questionable that chipmunks and probably other sciurids would act as suitable intermediate hosts for *Paruterina candelabraria*. Even if the tissue reaction of the host does not have a detrimental effect upon the cysticercoids, there would be relatively little opportunity for owls to become infected from squirrels, since these diurnal mammals do not form a very considerable part of their diet. It might be of some interest to attempt infection experiments with various species of shrews, especially *Blarina*. However, the few hundred shrews of various species for which we have records have disclosed no cestode larvae of this type.

SUMMARY

The life cycle of *Paruterina candelabraria* (Goeze, 1782), a cestode parasitic in owls, has been experimentally completed. Rodents serve as the intermediate host. Hamsters, white-footed mice, and laboratory mice were successfully infected, and the infection was transmitted to an owl by feeding heavily infected mice. The cysticercoids of *Paruterina candelabraria* develop in the

liver of the intermediate host. Histopathological changes resulting from infection with cysticercoids of *P. candelabraria* were compared with changes caused by larvae of other cestode genera, and were found to be similar.

ACKNOWLEDGMENT

The writer wishes to express his indebtedness to Dr. Louise A. Lombard for her aid in connection with the histopathological part of this work, and without which this work could not have been completed.

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A New Genus of the Subfamily Psammocharinae (Hymenoptera: Psammocharidae) with Descriptions of Eight New Species and a Key to the Species

R. R. Dreisbach
Midland, Michigan

The genus *Anopliella* was set up by Banks (1939) to include the species *Pompilus tenebrosus* Cresson (1867) which he made the genotype, and a new species *A. imbecilla* which he described at the time.

The new species was described from the female only and as far as the writer knows, no male of this genus has ever been described, since *P. tenebrosus* Cr. was also described from the female only. Dr. Banks, however, did name a number of specimens as the male sex, but these were mostly males of the genus *Pompilinus*. The females were separated from the rest of the tribe *Psammocharini* by the fact that the second joint of the anterior tarsi had a spine in the middle as long as that at the tip, marginal cell more than its length from the wing tip, and propodeum with upright hair. The spine at the middle of the second tarsal joint applies only to the females as the males do not have a tarsal comb.

When slides of the genitalia and last ventral plate were made it became evident that there were a number of species with very great similarity in the above mentioned parts, and that these species also could be distinguished from the genus *Pompilinus* (which it closely resembles by virtue of the marginal cell being more than its length from wing tip) by the fact that the claws of the anterior legs were split while the claws of the last two pairs of legs were not split but had a small tooth behind the long outer ray. Since the females do not have split claws, this character can not be used in that sex. *Pompilinus* and *Anopliella* were separated on the basis of the presence of upright hair on the propodeum (*Anopliella*) or the absence of such upright hair (*Pompilinus*) In the new species here described some have upright hair on the propodeum and some do not. For this reason, this character is certainly questionable as a means of distinguishing the females of these two genera. In Cresson's description of *tenebrosus,* he defnitely states that the third cubital cell is petiolate, and Banks (1939) in his description also states that *tenebrosus* has the third cubital cell petiolate, but that his new species, *imbecilla,* has a space between the second and third intercubital veins on the marginal vein. The new species here described, without exception, have such a space between these two veins on the marginal vein, while all the species which the writer believes to belong to the genus *Pompilinus,* including about seven new species to be described, have the third cubital cell either petiolate or sessile, i.e. the second and third intercubital veins meet on the marginal vein, except for one species where there is a very small space between these veins on the marginal. If *tenebrosus* is

placed in the genus *Pompilinus,* the character just mentioned makes a good separation of these two genera for the females with the difference of the claws making a better separation for the males.

Since *tenebrosus* is removed to the genus *Pompilinus,* and since it was the genotype of the genus *Anopliella* Banks, it becomes necessary to erect a new genus for this group of spider wasps. For this the writer proposes the name *Anopompilinus* and designates the species *A. michiganensis* n. sp. as the genotype.

The following key will then separate these two genera from each other:

1. Third cubital cell either petiolate or sessile on the marginal vein, or if a slight distance between these two veins on the marginal vein, it is much less than in the species in the next couplet; aroliae not so large and generally shorter than distance from the base of claw to the tooth; spines on posterior tibiae only about width of tibiae, all spines on tarsal joints longer than and more numerous than in the next couplet; male: claws of all the legs cleft or split; in most cases aedeagus flares out at tip, and is entirely free of any glandular protuberances on the sides or tip; parapenial lobes narrow and as long as aedeagus ..... *Pompilinus* Banks

1. Third cubital cell never petiolate or sessile, but always with a definite space between the second and third intercubital veins on the marginal vein; aroliae of claws larger than in the preceding and reaching to the small tooth on the claw; spines on posterior tibiae much shorter only about two fifths width of tibiae; spines on tarsal joints shorter and not so numerous as in the preceding; male: claws of only the anterior pair of legs split, the other two pairs with only a small tooth near the middle; aedeagus never flares out at the tip but has the sides straight and parallel, while the sides and sometimes the tip has small glandular protuberances, except in two species; parapenial lobes are very wide and not as long as aedeagus ..... *Anopompilinus* n. gen.

The genus is very close to *Pompilinus* but is distinctly different in a number of fundamental characters as shown in the key above. These characters can be seen better than described as the plates will demonstrate. Figures 22, 23 show the venation of the wings of *Anopompilinus michiganensis* n. sp., which is characteristic of all the species of the tribe *Psmmocharini,* and the nomenclature as given there is that used in this paper and which will be used in all future papers by the writer. Figure 24 gives the nomenclature as applied to the parts of the genitalia and is that used by Snodgrass (1941) in his paper on the genitalia of the Hymenoptera and also by Bradley (1944) in his paper on the Tribe Psammocharini.

The location of the types and paratypes is given after the name of the collector and the abbreviations used represent the following collections: MCZ, Museum of Comparative Zoology, at Harvard College; OSU, Ohio State University, Columbus, Ohio; MZUM, Museum of Zoology at the University of Michigan at Ann Arbor, Mich.; RRD R.R. Dreisbach collection, Midland, Mich.

Anopompilinus n. gen.

Entirely black insects, except the tips of mandibles are reddish and in one case the first two abdominal segments are red, with the size and general appearance of the genus *Pompilinus;* the tips of mandibles are reddish, with long scattering hairs borne on the basal half; similar long hairs on the men-

tum, which are for the most part very much exposed; aroliae of the claws larger than in *Pompilinus* and with a brush of thinly placed hairs borne on the base of aroliae and reaching to the tip of aroliae, which are as long as ray behind the tooth, these hairs longer in female than in male and generally longer than in the genus mentioned; third cubital cell of both sexes *never* petiolate or sessile, and very small and *always* shorter than the distance from its tip to the end of wing; the short marginal cell separates this genus from all related genera except *Pompilinus* (since other genera with short marginal cells are separated by other distinguishing characters), and the cell generally shorter and smaller and a greater distance from its wing tip than in that genus; tarsal comb in females varies from hardly width of anterior metatarsal joint to several times as long; in most cases propodeum does not have upright hair, but in other cases this upright hair is very evident; the males are distinguished by the last two pairs of tarsal claws having a small tooth about the middle instead or having the claws split;; sides of aedeagus straight and parallel and in most species the sides and often the tip have small gandular protuberances, which distinguish it from any other genera; parapenial lobes shorter than the aedeagus and much wider than in related genera; volsellae characteristic of the genus as can be understood much better by an inspection of the figures than by a description, as also applies to the parameres; last ventral segment of most species with one or more long hairs, extending downward at right angles to the segment; these hairs are located just before tip of segment, and often with one or more groups of long hair or bristles located near the base of the segment; this character is also unique to this genus. The size of the males vary as follows: length of head and thorax from 2.65 mm. to 4.97 mm., length of abdomen from 2.67 mm. to 5.6 mm., length of fore wing from 3.98 mm. to 7.94 mm., rear wing from 3.2 mm. to 5.96 mm. Females: length head and thorax from 3.0 mm. to 4.24 mm., abdomen from 3.0 mm. to 4.3 mm., fore wing from 5.17 mm. to 6.9 mm., rear wing from 3.64 mm. to 5.3 mm.

Genotype—Anopompilinus michiganensis n. sp.

Anopliella imbecilla Banks, belongs in this genus as it fits all the characters as given in the description of the genus. This is probably the female of one of the males described in this paper, but of which one is a question.

Pompilinus tenebrosus Cr. seems to possess the only female in that genus with upright hair on the propodeum—provided that all the specimens so named are in reality this species. The male *Pompilinus canadensis* Banks, also has these upright hairs on the propodeum in just about the same length and distribution and this is probably the male of *tenebrosus*. Most of the males placed under *tenebrosus* in the Harvard collection by Banks, are his species *canadensis*, based on genitalia, while the others are other species of *Pompilinus* that do not have the upright hair, but otherwise look exactly like them externally.

Anopompilinus coloradensis n. sp.

Figs. 16, 17

Holotype male.—Entirely black except tip of mandibles reddish; a few long hairs on clypeus, mentum, base of mandibles, vertex, and under side of head

and prothorax; clypeus truncate at anterior edge and when seen from side only slightly bulging; anterior ocellus a little more than its diameter from the lateral ocelli and these with the distance between them about equal to their distance from the eye margin; no sulcus from the anterior ocellus to the base of antennae; vertex very slightly raised at the ocellar triangle when seen from in front; first antennal joint equal to third in length, the rest of antennae lost; pronotum sharply angulate, a very few upright hairs on propodeum; the abdomen completely devoid of upright hair, but covered with very fine appressed, blackish hair; wings slightly yellowish all over, hardly more so at the tip than the rest; basal vein in fore wing slightly basad of the transverse, first recurrent meeting the second cubital cell about the middle, third cubital cell not petiolate but with its length on marginal vein about one third its length on the cubital vein, first intercubital sloping very strongly toward wing tip, thus making the first and second intercubital veins almost parallel in their upper half; in the rear wing the subdiscoidal vein arises beyond the cell; last ventral segment with a slight longitudinal ridge in middle and the whole surface covered with short hair, with several long hairs, about the width of segment at its tip, extending vertically downward from its ventral surface, this is characteristic of several of the species in the genus; there are no tufts of heavy hair (almost bristles) at the sides of the base of ventral surface of the last ventral as in the species *A. aspinosus;* aedeagus with several small spines or rather small glandular protuberances near the tip on the outer edges and partly on tip, this again is typical of most of the species in the genus; legs almost devoid of spines; longer spur of hind tibiae seven-tenths as long as the first posterior metatarsal joint; the anterior pair of claws split but the other two pairs with no evidence of split claws but with a small tooth.

Length: Head and thorax 2.85 mm., abdomen 3.00 mm., fore wing 4.64 mm., rear wing 3.64 mm., genitalia: width at base 0.66 mm., length 0.93 mm. Last ventral segment: width at base 0.33 mm., length 0.80 mm.

Holotype male: Florissant, Colo., VI 22, 1902, S. A. Rohwer (MCZ).

Anopompilinus anomalus n. sp.

Figs. 1, 2

Holotype male.—Completely black except for the tips of mandibles which are reddish; a few long hairs on vertex, front of clypeus, basal half of mandibles, and under side of head, rest completely devoid of long hair; head and thorax covered with short appressed glistening white hair, the abdomen with very little of this white hair; clypeus truncate in front and hardly bulging when seen from side; anterior ocellus a little more than its diameter from the lateral ocelli and these with the distance between them slightly less than their distance from eye margin; no sulcus from anterior ocellus to base of antennae; vertex straight across when seen from in front; first, third and fourth antennal joint subequal, the joint beyond the sixth missing; pronotum arcurate with a slight angulation at its center; no upright hair on propodeum; wings slightly brownish, slightly darker at tips; first recurrent vein received by the second cubital cell about basal third, second recurrent received by the third cubital cell about the middle, second cubital cell one third as long on marginal veins as it is on the cubital vein, both first and second inter-

cubitals sloping forward; marginal cell exceedingly small, its distance from wing tip equal to three times its length, basal vein also interstitial in one wing and slightly basad of the transverse vein in the other wing, in rear wing the subdiscoidal vein arises beyond the cell; last ventral segment slightly roofshaped and with a few long hairs extending downward as in *A. coloradensis;* with a very long fringe of hair on each side of this segment extending from base to slightly beyond middle, these long thin hairs are not heavy, almost spine like as in *A. tenebrosa;* legs with very few spines; longer spur of hind tibiae about two-thirds as long as the posterior metatarsal joint; fore claws split, the other two pairs with their ends broken off.

Length: Head and thorax 2.65 mm., abdomen 2.67 mm., fore wing 3.98 mm., rear wing 3.2 mm., width last ventral at base 0.26 mm., length 0.53 mm., genitalia width at base 0.53 mm., length 0.795 mm.

Holotype male: Mountain Home Lake, Fort Garland, Colo., VII 20-25, 1932. Ele. 8300 ft. (MCZ).

Anopompilinus occidentalis n. sp.

Figs. 27, 28

Holotype male.—Completely black; a few long hairs on clypeus, vertex, under side of head, anterior side of fore coxae, dorsal surface of pronotum and propodeum, and at apex of last tergite; clypeus truncate and with a slight bulge when seen from side; anterior ocellus twice its diameter from the lateral ocelli and these with the distance between them equal to their distance from the eye margin; no sulcus but a faint line extending forward from the anterior ocellus; vertex straight across when seen from in front; third antennal joint slightly longer than the first and about equal in length to the fourth joint; pronotum strongly angulate, no sulcus on propodeum, and no upright hair; the first and second recurrent veins meeting the second and third cubital cells respectively in the middle; second cubital cell two-fifths as long on marginal vein as on the cubital vein, third cubital cell one-fourth as long on marginal vein as on the cubital vein; basal veins in forewings interstitial, and the subdiscoidal vein in rear wings arising slightly beyond the cell; marginal cell about its length from wing tip; whole wing brownish; last ventral segment with four or five long hairs (almost spines) extending downward at right angles from slightly before the tip of segment, these about one and one half times as long as width of ventral at apex, the whole ventral surface of this segment hispid; genitalia has the parameres slightly narrower near base than in the upper region, the sagittae are somewhat sickle shaped and the spiniferous protuberances extend down the side almost to base.

Length: Head and thorax 3.45 mm., abdomen 3.6 mm., fore wing 5.66 mm., rear wing 4.6 mm., genitalia width 0.66 mm., length 1.26 mm., last ventral segment width 0.46 mm., length 0.994 mm.

Holotype male: Pinecrest, Tuolumne Co., Cal., VII-29-47, P. H. Arnaud, Jr. (MCZ).

Paratypes: Pinecrest, Tuolumne Co., Cal., VII-28-29-47, J. H. Arnaud, Jr.. (RRD) Bedwer Canyon, Utah, VII-12, G. F. Knowlton (OSU).

This species is similar to *A. banksi* but the genitalia is fifty per cent larger, it has one or more fine spines on last ventral, the parapenial lobes are much

more slender and somewhat sickle shaped, the aedeagus is of slightly different form, the glandular protuberances on aedeagus extend a longer distance down the sides, and the parameres are narrower at base than at apex whereas in *banksi* these are of about equal width throughout.

Allotype female.—Completely black except for a very small linear dash on posterior orbits close to and just below the top of eye, and a reddish spot about the middle of mandibles; long, scattered black hair on vertex, front, clypeus, anterior surface of fore coxae, even more sparsely located ones on the ventral surface of abdomen, and with somewhat shorter ones on pronotum, dorsal surface and dorsal edge of propodeum and the apical tergite; a few closely appressed white hairs on the sides of face to just above antennal fossae, and anterior and posterior orbits; the rest of head and thorax with closely appressed brownish pubescence, that does not show up as glistening in reflected light; clypeus, when seen from the side, with considerable of a bulge, greatest about the middle but still raised at the anterior edge so as to make the front edge of clypeus slightly incurved; vertex, when seen from in front, with just an indication of a bulge at ocellar triangle, while when seen from the side, the front from just in front of anterior ocellus to antennal fossae is barely elevated above eyes; a slight depression just in front of the anterior ocellus, and a faint indication of a line to antennal fossae, which is plainly evident just before fossae; anterior ocellus less than its diameter from the lateral ones and these about as far apart as their distance to eye margin; antennae long and slender, third joint longer than the first and second combined, subequal to the fourth and fifth and twice as long as ultimate segment; first antennal joint with a few upright hairs on anterior surface; posterior orbits widest slightly below the middle and the width at this point slightly less than width of eye; pronotum slightly angulate; comparative lengths of pronotum, mesomotum, scutellum, and postscutellum are 8-15-9-3; posterior surface of propodeum nearly vertical and slightly concave at center; abdomen short and segments telescoped within each other; basal segment entirely free of upright hair; wings strongly fuliginous, slightly darker beyond the cells; marginal cell very short, only about one half as long as its distance to wing tip; third intercubital vein bends out and then in so that the length of third cubital cell on the marginal vein is only about one-third that on the cubital vein; second cubital cell about one half as long on marginal as on cubital; first recurrent vein is received by the second cubital cell beyond the middle and the second recurrent received by the third cubital cell at middle; basal vein slightly basad of the transverse median, and the subdiscoidal vein in rear wing arises beyond the cubitus; fore legs with a long tarsal comb, as long as genus *Psammochares*, with three spines on fore metatarsal joint; a very few long hairs on fore femur, and a few even shorter ones on the other two pairs; no spines on fore femur and only a few tiny ones on the dorsal surface of the other two pair; a few tiny spines on anterior edge of fore tibiae and three very long ones and a shorter one on posterior edge, besides the very long one at tip on ventral edge; a small indentation and a few fairly long spines around tip; posterior two pairs with numerous shorter, thicker spines on all surfaces; tarsal joints well spined; fourth joint of fore tarsi is very small and only about one half as long as third joint, while this joint in last two pairs is two-thirds as long as third joint; claws of all

legs similar, with a small tooth slightly beyond middle of claw, with two or three long hairs arising from base of this tooth and extending to tip of claw; aroliae comparatively large, and extending to about the location of the tooth, larger in the fore legs; a thin brush of 10-12 hairs arising from base of dorsal surface of aroliae, and as long as aroliae; longer spine of hind tarsi two-thirds as long as the posterior metatarsal joint.

Length: Head and thorax 3.97 mm., abdomen 2.65 mm. (telescoped so this length is misleading), fore wing 6.30 mm., rear wing 4.97 mm.

Allotype female: Pinecrest, Tuolumne Co., Cal., VII-29-47, acc. no. 46, P. H. Arnaud, Jr., (MCZ).

This may not be the female of *occidentalis* but both were collected at the same place at the same time, both have upright hair on the propodeum, both are long winged, and both have similar venation.

Anopompilinus dakota n. sp.

Figs. 9, 10

Holotype male.—Completely black, except a slight amount of reddish at tips of mandibles; a few long hairs on vertex, clypeus, basal half of mandibles, and under side of head and pronotum; clypeus truncate and slightly bulging, when seen from the side; head thorax, and coxae covered with fine, appressed, brownish hair; anterior ocellus about twice its diameter from the laterals and these about as far apart as their distance from eye margin; no sulcus extending forward from anterior ocellus but a very faint line extending to base of antennae; a very faint bulge at the ocellar triangle when seen from in front; third and fourth antennal joints subequal and longer than the first; pronotum only very slightly angulate, the propodeum with only closely appressed hair; no sulcus on propodeum; wings brownish all over; second recurrent vein meeting the third cubital cell at middle, the first recurrent vein meeting the second cubital cell at apical third; second and third cubital cells of about equal length on marginal vein, but the third cell slightly longer on the cubital vein; marginal cell one and one half times its length from wing tip; basal vein slightly basad of the transverse median vein in fore wings and the subdiscoidal vein arise slightly beyond cell in the rear wings; last ventral segment with a long spine near the tip extending downward at right angles and about equal in length to the width of segment.

Length: Head and thorax 3.32 mm., abdomen 3.5 mm., fore wing 4.70 mm., rear wing 4.0 mm., length of genitalia 0.927 mm., width 0.596 mm., length last ventral 0.596 mm., width 0.33 mm.

Holotype male: Stump Lake, Nelson Co., N. Dak. VII-7-20, T. H. Hubbell (MZUM).

Anopompilinus banksi n. sp.

Figs. 11, 12

Holotype male.—Completely black, except for reddish on the tips of mandibles; a few long light colored hairs on vertex, basal half of mandibles, under side of head and posterior orbits, the hairs on front part of posterior orbits darker than those on upper posterior orbits and behind the head; a few long

hairs also on propodeum; the whole thorax and most of coxae covered with fine, closely, appressed, white sericeous hair, with a few sparse ones on head; clypeus truncate and almost flat when seen from side; the anterior ocellus twice its diameter from the lateral ocelli and these slightly closer to each other than to the eye margin; antennae very slender, the third joint slightly longer than the first and about equal to the fourth in length; pronotum angulate, a sulcus on dorsal surface of propodeum, much deeper at base and fading out at apex of dorsal surface; first recurrent vein meeting the second cubital cell near the middle, second recurrent vein meeting the third cubital cell much before the middle, near basal third; third intercubital vein sloping inward and thus the third cubital only about one-third as long on marginal vein as on cubital vein, and only about one half as long on marginal vein as the second cubital cell, the two cells of about equal length on the cubital vein; basal veins only very slightly disjointed, the basal being slightly basad of the cubital vein; the subdiscoidal vein in the rear wings interstitial with the transverse; the whole wing brownish all over but slightly darker at tip; marginal cell slightly more than its length from wing tip; only a very small spine or long upright hair on last ventral segment; longer spur of hind tibiae about two-thirds the length of posterior metatarsal joint. The paratypes have a very evident long spine on last ventral segment.

Length: Head and thorax 3.12 mm., abdomen 3.7 mm., fore wing 4.64 mm., rear wing 3.64 mm., genitalia width at base 0.46 mm., length 0.86 mm., last ventral segment width at base 0.33 mm., length 0.86 mm.

Holotype male: Luce Co., Mich. VII-5-46, R. R. Dreisbach (MCZ).

Paratypes: Cornwall, Vt., VI-13-36, Richard Dow (MCZ), Lapeer Co., Mich. V-30-37, R. R. Dreisbach (RRD), Cheboygan Co., Mich., VIII-31-40, R. R. Dreisbach (RRD).

The Michigan paratypes vary in size as follows: Length of head and thorax from 3.1 mm. to 3.2 mm., abdomen both 3.00 mm., fore wing 4.63 mm. to 4.70 mm., rear wing from 3.64 to 3.70 mm. The Vermont paratype is somewhat larger, in wing spread particularly, length of head and thorax 3.31 mm., abdomen 3.40 mm., fore wing 5.30 mm., rear wing 4.20 mm. While the size in this particular specimen differs from the type more than the other paratypes, yet the genitalia and last ventral segment place it definitely as this species. All the specimens except the Cheboygan Co. specimen have upright hair on the propodeum.

Anopompilinus michiganensis n. sp.

Figs. 20—24, 29, 30

Holotype male.—Completely black except the tips of mandibles are reddish; a very few long hairs on mentum, basal half of mandibles, one or two on vertex, and a few long whitish hairs on the underside of head, no long hairs on the clypeus or any other part of body; clypeus truncate, with only a very slight bulge when seen from the side; the front just behind the insertion of antennae raised considerably above the level of the eyes; ocelli in an equilateral triangle, the posterior pair as far apart as their distance to the eye margin; vertex almost straight across when seen from in front; a faint line extending from the anterior ocellus to the insertion of the antennae; antennae slender, as it is in all the genus, the first and third joints subequal in length and the second joint one half as long as the first, no upright hair on the first joint; pronotum sharply angulate, no upright hair on the propodeum; abdomen covered with very

fine, closely appressed, slightly shining hairs, the whole body with this same slightly shining appearance; wings slightly brownish all over but more strongly so at the tip beyond the cubital cells; basal vein of fore wing slightly basad of the transverse vein, first recurrent vein meeting the second cubital cell at the apical third, second recurrent vein meeting the third cubital cell at the middle; third cubital cell with its length on the marginal vein about one-third its length on the cubital vein, the second cubital cell with its length on the marginal vein about one half its length on the cubital vein; in the rear wing the subdiscoidal vein arises much beyond the cell; last ventral segment with a number of long hairs extending downward from the segment, all arising from the same point near the tip of segment; the central part of this segment with an elevated rather flat surface extending from the base to about the location of the long hairs, the sides and tip beyond the hairs sloping downward at an obtuse angle from this elevated portion, a slight swelling at the center of base; the genitalia has a tuft of heavy hairs or bristles on each side of the base, very similar to those of the species *A. aspinosus* n. sp.; longer spur of posterior tibiae three-fourths the length of the posterior metatarsal joint; fourth joint of fore tarsi about as long as the third joint, the fourth joint of posterior tarsi about five-eighths as long as the third joint.

Length: Head and thorax 3.32 mm., abdomen 4.0 mm., fore wing 5.3 mm., rear wing 4.0 mm., genitalia length 0.927 mm., width 0.662 mm., last ventral length 0.994 mm., width 0.463 mm.

Holotype male: Branch Co., Mich., V-31-42, R. R. Dreisbach (MCZ).

Paratype males: Midland Co., Mich., VIII-25-45, R. R. Dreisbach (RRD), Wayne Co., Mich., VI-4-38, G. Steyskal (RRD), Livingston Co., Mich., VII-30-39, R. R. Dreisbach (RRD), Shiawasse Co., Mich., VII-13-43, R. R. Dreisbach (RRD), Jackson Co., Mich., V-30-42, R. R. Dreisbach (RRD), Cornish, N. H., VII-13-08, C. W. Johnson (MCZ).

All the paratypes agree with the type in the absence of upright hair on the propodeum, and they vary in size as follows: length of head and thorax 3.31 mm. to 3.40 mm., abdomen 3.5 mm to 4.0 mm., fore wing all 5.3 mm., rear wing all 4.0 mm. This species is very close to *A. aspinosus* n. sp. but is smaller in every way. The last ventral segment has one or more long hairs arising from near the tip whereas *A. spinosus* has none, otherwise the last ventral is similar but smaller.

Anapompilinus aspinosus n. sp.
Figs. 5, 6

Holotype male.—Completely black, except a slight indication of reddish on the first two abdominal tergites and the apical half of the mandibles are reddish; the only real long hairs are those on the middle third of the mandibles, the apical third almost bare and the basal third covered with closely appressed brownish hair, and a very few longer hairs, but these much shorter than those on middle third; a very few long hairs on vertex, mentum and more scattered on mesonotum, rest of body devoid of long hair; clypeus when seen from the side convex, slightly, evenly, arched from base to tip where it is truncate, the whole surface except edge at front covered with the same appressed, brownish hair as the base of mandibles; the face to just above the antennal fossae with appressed silvery hair, the front and vertex without these appressed silvery hairs, but with brownish very short hair, but without the mat appearance of the

silvery hair on face; vertex when seen from in front with a very slight bulge at ocellar triangle; a very faint line from anter ocellus to antennal fossae; fore ocellus its diameter from the lateral ones and these slightly nearer to each other than to the eye margin; posterior orbits very narrow; first joint of antennae slightly shorter than the third and fourth which are subequal, the basal joint with closely appressed, somewhat shining, brownish hair on the front; antennae beyond the fourth joint lost; pronotum conspicuously angulate; dorsum of thorax, including the scutellum and post scutellum, covered with the appressed brownish hair of parts of head, while the dorsum and sides of propodeum and thorax have these hairs silvery; propodeum without a trace of upright hair, wings slightly fuliginous all over but more so from end of cells to tip; first recurrent vein meets the third cubital cell before the middle; both the first and third intercubital veins curving very strongly toward each other, thus both the second and third cubital cells only about one-third as long on the marginal vein as they are on the cubital vein; the basal vein in fore wings slightly basad of transverse median vein, and the subdiscoidal and cubital veins in rear wings interstitial, the abdomen covered with finely appressed brownish hair; longer spur of posterior tibiae four-fifths as long as the posterior metatarsal joint; fourth tarsal joint of anterior tarsi, two-thirds as long as third tarsal joint, third joint of posterior tarsi about one half as long as third joint; last ventral segment without a spine, but with a short, compact row of long hair each side at base of segment, very much like *A. michiganensis* n. sp. but larger in all measurements than that species, and without the spine of that species.

Length: Head and thorax 4.24 mm., abdomen 4.30 mm., fore wing 6.9 mm., rear wing 5.3 mm., genitalia length 0.994 mm., width 0.729 mm., last ventral length 0.994 mm., width 0.464 mm.

Holotype male: Alcona Co., Mich., VII-31-38, R. R. Dreisbach (MCZ).

This species very similar to *A. michiganensis,* but the genitalia and last ventral segments are of different size and apsinosus has a spine on the last ventral segment and the comparative sizes of tarsal joints are different; the third tarsal joint of anterior tarsi is about as long as third joint and the third tarsal joint of posterior tarsi is about five-fifths as long as fourth joint in *michiganensis* while in aspinosus they are as shown above.

Allotype female.—Black, except the first two abdominal segments are almost entirely light red, the mandibles except base are a light red color, and the anterior part of clypeus, except a black anterior border, is slightly reddish; a very few scattered, long, black hairs on vertex, clypeus, pronotum, and last dorsal segment, but these hairs present in greater numbers on the basal two-thirds of mandibles, posterior orbits, fore coxae, lower anterior edge of pronotum, and ventral surface of abdomen; a few long white hairs on neck just back of head and on the lower back edge of head; the whole body and legs clothed with brownish slightly sericeous, closely appressed hair; the clypeus, when seen from the side, with a slight bulge; when seen from above, the anterior edge is definitely incurved, concave almost emarginate; the anterior edge with a narrow, smooth, black border back of which is a slightly reddish portion which is about

twice as wide as border in center and broadening out to about four times as wide as border at the sides, the rest of clypeus black; vertex when seen from in front, straight across, and when seen from the side, the vertex is even with the eyes, but the front rises slightly to a peak at antennal fossae, which is above the surface and somewhat higher than in the species *A. occidentalis* n. sp.; anterior ocellus more than its diameter from the lateral ocelli, and these about as far from the edge of eye as from each other; a slight depression just before the anterior ocellus and a very faint line extending forward which becomes more evident just before the antennal fossae; posterior orbits broadest below the middle, not quite as wide as eyes; pronotum hardly angulate, borderline; propodeum without any upright hair on dorsal surface but a few short upright ones on dorsal edge; comparative lengths of pronotum, mesonotum, scutellum, and postscutellum are 25—40—30—7; basal, dorsal, inclined surface of first tergite black, remainder light red, second tergite same color and third tergite with a small median triangle and dorsal anterior edge a light reddish; marginal cell small, more than its distance from wing tip; first intercubital vein sloping backward, so that the second cubital cell is two and one-half times as long on the cubital vein as on the marginal; the third intercubital vein is straight for a short distance and then slopes forward so that the third cubital cell is about four times as long on the cubital vein as on the marginal; second intercubital vein is inclined slightly backward; first recurrent vein is received about the middle by the second cubital cell, and the second recurrent before the middle of the third cubital cell; basal vein slightly basad of the transverse median vein; subdiscoidal vein in rear wings is slightly beyond the cubitus; very few hairs on any of the femur, and only a very few tiny spines; anterior tibiae with only two or three tiny spines on anterior edge, but three long ones on the posterior edge, with the usual large, apical, ventral spine and two shorter apical spines; last two pairs of tibiae with fairly long spines on all surfaces, besides the two long spines at tip; fore metatarsal joint with three spines about as long as width of joint, second and third joints with a similar spine in middle of same length, in other words, a very short tarsal comb; remainder of tarsal joints heavily spined as usual; fourth joint of fore tarsi almost as long as third joint which is short, the fourth joint of last two pairs of tarsi only about one half as long as third joint, and the third joint of these pairs about twice as long as the third joint of first pair; aroliae exceptionally large; longer spur of posterior tibiae about two-thirds as long as posterior metatarsal joint;

Length: Head and thorax 3.00 mm., abdomen 3.00 mm., fore wing 5.17 mm., rear wing 3.64 mm.

Allotype female: Fleetwood, Schoolcraft Co., Mich., F. M. Gaige, No. 18, VII-4-15 (MZUM).

This resembles *Pompilinus autumnalis* superficially, in having the first two abdominal segments red, but differs in the very much curved anterior edge of clypeus, the much shorter spines on the last two pairs of tarsal joints, the longer aroliae which reach to the tooth of claws, while the aroliae of *autumnalis* do not reach the tooth. While the second and third intercubital veins do not quite meet on the marginal vein in *autumnalis*, they are very much closer than in this new species.

Anopompilinus hirsutus n. sp.

Figs. 18, 19

Holotype male.—Head missing; completely black; long hair on under side of pronotum and a very few short upright hairs on propodeum; pronotum almost transverse but with a very slight angulation in the middle; a very short sulcus on dorsal surface of propodeum; abdomen except the last ventral segment almost devoid of hair except the very short, closely compressed, hair which covers the whole surface and a very few short hairs at the vertex of last tergite; the wings brownish all over; the second recurrent vein enters the third cubital cell slightly before the middle, the first recurrent vein meets the second cubital cell beyond the middle; the third cubital cell only about one-third as long as the marginal vein as on the cubital vein; second cubital cell slightly more than one and one half as long on cubital vein as on the marginal vein; basal vein slightly basad of the transverse cubital vein in fore wings and the subdiscoidal and cubital veins are interstitial in the rear wings; longer spur of hind tibiae about two-thirds as long as posterior metatarsal joint; last ventral segment has long hairs projecting from the edge from about the middle of the segment to around the tip, this is very characteristic of this species and of *A. mainensis* n. sp.; this segment has more long hair extending at right angles to the segment than any other species except the one mentioned above; these hairs, almost bristles arise from the middle of the segment and extend over the apical half.

Length: Thorax 2.65 mm., abdomen 3.31 mm., fore wing 5.66 mm., rear wing 4.2 mm., genitalia length 1.00 mm., width 0.66 mm., last ventral length 0.86 mm., width at base 0.33 mm.

Holotype male: Estes Park, Colo., VII-14-34, A. L. Melander (MCZ).

This species is almost like *A. mainensis* n. sp. in the appearance of the genitalia and last ventral except in size and the fact that the last ventral is much more pointed at the apex than in *mainensis* which is obtuse. This species is much larger in every respect and the differences between it and *mainensis* are indicated in the key.

Anopompilinus mainensis n. sp.

Figs. 25, 26

Holotype male.—Completely black, except tip of mandibles which are reddish, and a very short narrow white spot at edge on posterior orbits about one-fourth of the way from top; long hair on vertex, front, mentum, base of mandibles, posterior orbits (more numerous here than elsewhere) front of fore coxae, pronotum, and a few shorter ones on the dorsal edge of propodeum; clypeus, when seen from the side slightly arched, the anterior edge slightly concave; the vertex, when seen from in front is straight across, without bulge; fore ocellus about one and one half times its diameter from the lateral one and these as far apart as the distance between them and the eye; head, when seen from side, with the vertex and about half the distance to the antennal fossae on the same level as the eyes, but sloping above eye level from there to antennal fossae; a very short sulcus just behind antennal fossae, and just

back of this a very short raised, shining line; posterior orbits with their upper three-fourths about of equal width and just as wide as eyes; mentum exposed and a broad shallow sulcus longitudinally; antennae missing; clypeus and face to top of antennal fossae covered with rather long, closely appressed, silvery pubescence, and the posterior orbits showing a trace of silvery in reflected light; pronotum angulate; closely appressed, very short, brownish hair on thorax, coxae and on most of the legs; propodeum forms a smooth curve from front to apex; wings brownish all over but darker beyond the cells; first recurrent vein meets the second cubital cell at apical third, the second recurrent meets the third cubital cell before the middle; third intercubital vein curves forward very strongly so that the second and third intercubital veins are very close together on the marginal, only about the thickness of a vein between them; second cubital cell about two-thirds as long on cubital vein as the third cubital cell, and this cell is only slightly longer on the cubital vein than on the marginal vein; basal vein strongly basad of the transverse median vein in fore wings and the subdiscoidal in rear wings is quite a distance beyond the cubitus; the only perfect leg is the right mesothoracic and this has the third tarsal joint one and one half times as long as the fourth tarsal joint; middle tibiae not nearly so heavily spined, nor with such long spines as in species *A. hirsutus* n. sp.; longer spur of hind tibiae about two-thirds as long as the posterior metatarsal joint; last ventral segment and genitalia similar to those of *hirsutus* as noted elsewhere.

Length: Head and thorax 4.97 mm., thorax 3.95 mm., abdomen 5.6 mm., fore wing 7.94 mm., rear wing 5.96 mm., genitalia length 1.325 mm., width 0.86 mm., last ventrite length 1.10 mm., width 0.40 mm.

Holotype male: Bangor, Me., VII, F. A. Eddy (MCZ).

This species is almost identical with *A. hirsutus* except for size and the difference given in key, as well as for the fact that at present the one is known from the East and the other is Western.

In addition to these new species there are two species described by Banks in the genus *Pompilinus* which belong here if the key previously given for separating the genera *Pompilinus* and *Anopompilinus* is followed. These two species are *Pompilinus parvulus* Banks, and *P. solonus* Banks. The first was described from both male and female while the second is known only from the female. A redescription of these follows, as well as a redescription of the female of *A. imbecilla* and a description of the male of *imbecilla* which was never described.

ANOPOMPILINUS PARVULUS (Banks)

Fig. 14

Pompiloides parvulus Banks, Jr. N. Y. Ent. Soc. 19, 1911, p. 227. Male, female. (o.d. Colo. MCZ).

Psammochares angularis Banks, Jr. N. Y. Ent. Soc. 18, 1910, p. 115. Male. (o.d. Cal., MCZ).

Lecto-Allotype female.—A few long hairs on vertex, clypeus, mandibles, and on ventral surface of abdomen; clypeus truncate, flat, with a smooth front edge; fore ocellus twice its diameter from the laterals and these as far apart

as their ristance to eye margin; no line or suclus on front; vertex straight across when seen from in front; pronotum arcuate and no upright hair on propodeum; second cubital cell one and one half times as long on cubital vein as the third cubital cell, and the third slightly longer on the marginal vein than the second cell; second cubital cell one-fourth to one-fifth as long on marginal vein as on the cubital vein, third cubital cell one-fourth as long on marginal vein as on cubital vein; the distance from marginal cell to wing tip three times as long as the marginal cell, the tip of wing beyond the cells just under one-third the length of the whole wing; wings brownish but the tips darker beyond the cells; first recurrent meets the second cubital cell beyond the middle, and the second recurrent meets the third cubital cell a little before the middle; a short tarsal comb; fore coxae very large for so small an insect.

Length: Head and thorax 2.65 mm., abdomen 2.32 mm., fore wing 4.64 mm., rear wing 3.00 mm.

Lecto-allotype female: Piedmont, Colo., VI-2-02, S. A. Rohwer (MCZ).

Another female, not a paratype, from Laramie, Wyo., VI-6-08, S. A. Scullen. Two males at Harvard are this species: Bemington, Me., IX-6-20, A. P. Morse, and S. Newfane, Vt., VII, Miss Bryant. All the specimens of parvulus and angularis are from the far west except these two, but I can see no differences in either the genitalia or last ventral.

Male.—Similar but smaller; length of head and thorax 2.0 mm., abdomen 2.32 mm., fore wing 3.45 mm., rear wing 3.00 mm.; marginal cell one-third as wide as long; length of genitalia 0.464 mm., width 0.398 mm., length of last ventral 0.464 mm., width 0.20 mm. The length of the last venterite is not the whole length to end of spur as that is broken off, but is the length to the end of broad base where the spur starts.

Lecto-holotype male: Boulder, Colo., VI-1-02 (MCZ).

Paratype male: Boulder, Colo., VI-6-08, S. A. Rohwer (MCZ).

ANOPOMPILINUS SOLONUS (Banks)

Pompiloides solonus Banks, Jr. N. Y. Ent. Soc. 22, 1914, p. 303. Female. (o.d. Ariz. MCZ).

Lectoholotype female.—Long hair on head, mandibles, fore coxae, posterior orbits, neck, pronotum, a few on mesonotum and last ventrite, none on propodeum; clypeus truncate with a smooth edge, not bulging when seen from side; vertex straight across, when seen from side, and the whole front and antennal fossae level with the eyes; a line from fore ocellus to the antennal fossae; fore occelus its diameter from the laterals and these as far apart as their distance to eye margin; pronotum slightly angulate; wings brown all over; third cubital cell not petiolate, and slightly longer on the marginal vein than the second cubital cell and the two cells of about equal length on the cubital vein; third cubital cell one half as long on marginal as on the cubital; first recurrent vein meets the second cubital cell beyond the middle and the third recurrent vein meets the third cubital cell slightly before the middle; basal vein slightly before the transverse median, and in the rear wings the discoidal is considerably beyond the cubital; tarsal comb short, just about the width of tarsal joint; no spines on femur and very few on tibiae, fourth joint of posterior tarsi five-sevenths as long as the third joint; longer spur of posterior

tibiae four-fifths as long as posterior metatarsal joint; the third joint of antennae is slightly longer than the first.

Length: Head and thorax 4.00 mm., abdomen 4.40 mm., fore wing 6.95 mm., rear wing 56.3 mm. Paratype has the same measurements.

Lecto-holotype female: Garces, Ariz., VIII, N. Banks (MCZ).

Paratype: Little Tesuque Canyon, vic. Sante Fe, N. Mex., Alt. 9200', VII-27-32.

ANOPOMPILINUS IMBECILLA (Banks)

Figs. 13, 15

Anopliella imbecilla Banks, Can. Ent. 71, 1939, p. 227. Female. (o.d. Conn., Nova Scotia, Me. MCZ.)

Lecto-holotype female.—Second cubital cell as long on the marginal vein as the second, and one-third as long on marginal vein as on the cubital; :narginal cell two-thirds as long as its distance to wing tip; length of head and thorax 4.40 mm., abdomen 3.9 mm., fore wing 6.95 mm., rear wing 5.63 mm. Colebrook, Conn., IX-17-11, W. M. Wheeler.

Lecto-holotype male.—There is almost nothing left of this male except the thorax, wings, part of abdomen and genitalia; length of fore wing 4.77 mm., rear wing 4.00 mm.; the wings as described for female; length of genitalia 0.928 mm., width 0.596 mm., length of last ventrite 0.861 mm., width 0.33 mm.; the last ventral has a slight ridge almost its whole length, with a few hairs almost at tip longer than the rest.

Lecto-aloltype male: Bar Harbor, Me. (MCZ).

Paratype male: Mt. Desert Is., VII-4, C. W. Johnson (MCZ). The measurements of the genitalia of this specimen are: length of genitalia 0.93 mm., width, 0.53 mm., length of last ventral 0.93 mm., width 0.40 mm.

KEY TO THE SPECIES OF THE GENUS ANOPOMPILINUS N. GEN.

1. Females 2
1. Males 6
2. A very long tarsal comb, much longer than the width of tarsal joint ....*occidentalis* n. sp.
2. A short tarsal comb, just about as long as the width of tarsal joint 3
3. Abdomen with the first and second segments and the apical half of mandibles red .....*aspinosus* n. sp.
3. Abdomen black 4
4. Marginal cell very large, just about as long as its distance from wing tip; longer spur of posterior tibiae about two thirds as long as the posterior metatarsal joint; head and thorax 4.0 mm., abdomen 4.6 mm., fore wing 6.95 mm., rear wing 5.3 mm. .....*imbecilla* (Banks)
4. Marginal cell considerably shorter than its distance to wing tip, only about one half as long or less 5
5. Marginal cell very small, only about one third of its distance to wing tip, wings not very dark, darker at tip; pronotum arcuate; a very small species, head and thorax 2.65 mm., abdomen 2.0 mm., fore wing 4.30 mm., rear wing 3.3 mm. ....*parvulus* (Banks)

5. Marginal cell longer, about one half as long as its distance to wing tip, size much larger ..... *solonus* (Banks)

6. The apical half of last ventral segment with a median row of long bristles 7

6. Last ventral segment without a row of median bristles. but with these hairs or bristles if present, arising from one spot 8

7. Pronotum angulate; size very large, fore wing about 8.0 mm. long, rear wing almost 6.0 mm.; second and third intercubital veins with only about the distance of a vein between them on the marginal vein; last ventral segment obtuse and larger than the following; spines of tibial joints not so many nor so large as the following ..... *mainensis* n. sp.

7. Pronotum almost transverse; size smaller, fore wing under 5.7 mm., rear wing under 4.3 mm.; second and third intercubital veins with much more distance between them on the marginal vein; last ventral segment not so obtuse but almost acute ..... *hirsutus* n. sp.

8. Marginal cell very small, at least three times its length from wing tip and twice as long as wide, about 0.45 mm. wide; the second and third intercubital veins very close together on the marginal vein; pronotum transverse, with a very slight indication of an angulation behind; no long hair near tip at right angles to last ventral segment, but with a row of long hair each side at base, these hairs with small round knobs at tips; the whole genitalia with an entirely different aspect than that of any other species ..... *anomala* n. sp.

8. Marginal cell larger, no more than twice its length from wing tip, generally one and one half times its length, or if marginal cell is shorter, then the parameres are of an entirely different shape and the last ventral segment does not have any long hair near base; if hairs are present on the last ventral segment near base they do not have the small knobs at tips 9

9. Length of abodmen not more than 3.0 mm., fore wing less than 5.0 mm. and rear wing less than 4.0 mm., *and* pronotum angulate; a few fine bristles on last ventral segment at right angles hardly visible in photo; long hairs or bristles on each side near base of last ventral segment, not in a linear row but located more as a patch than a row ..... *coloradensis* n. sp.

9. Size larger *or* pronotum arcuate, *and* no long hairs or bristles on last ventral segment 10

10. Size about as in first couplet of 7 *but* pronotum arcuate *and* no long hairs or bristles on last ventral segment as in that couplet; last ventral segment very small and not very wide and somewhat wedge-shaped ..... *parvulus* (Banks)

10. Size much larger 11

11. A line from anterior ocellus to antennal fossae; no sulcus and no upright hair on propodeum; last ventral segment with a long spine, and with a few long hairs on each side, located in two separate rows ..... *dakota* n. sp.

11. No long hairs on each side of last ventral segment, separated in two long rows 12

12. Fore wing not over 4.8 mm. long 13

12. Fore wing 5.3 mm. or more in length 14

13. A sulcus on dorsal surface of propodeum; first recurrent entering the second cubital cell before the middle of cell; a spine on last ventral segment, located just anterior to the tip; marginal cell slightly more than its length from wing tip; parapenial lobes almost as long as aedeagus ..... *banksi* n. sp.

13. Marginal cell about two third of its distance to wing tip; parameres not so wide and parapenial lobes as long as aedeagus; last ventral segment slightly more pointed ..... *imbecilla* (Banks)

14. Four or five long bristles on last ventral segment, no tuft of long hair on each side of this segment near the base; thick part of parameres broader on apical half than on basal half; spinules on aedeagus extending downward on the sides almost to the base; aedeagus broader in the middle than that of any other species; last ventral segment slightly emarginate at tip ..... *occidentalis* n. sp.

14. One bristle or none on last ventral segment, a tuft of long, stiff hair or almost spines on each side near base 15

15. No long hair on last ventral segment near tip; larger than the following species, length of head and thorax 4.30 mm., abdomen 4.30 mm., fore wing 6.62 mm., rear wing 5.17 mm. ..... *aspinosus* n. sp.

15. A number of long hairs near tip of last ventral segment; smaller than the preceding species, length of head and thorax 3.60 mm., abdomen 3.60 mm., fore wing 6.30 mm., rear wing 4.63 mm. ..... *michiganensis* n. sp.

Since this paper was written, the following paratypes were found in other collections: *A coloradensis*, Sowbelly Canon, Sioux Co., Neb. VIII-19-12, G. W. Dawson (Uni. Neb.). *A michiganensis*, Monroe Canyon, Sioux Co., Neb. VIII--19-18, G. W. Dawson (Uni. Neb.).

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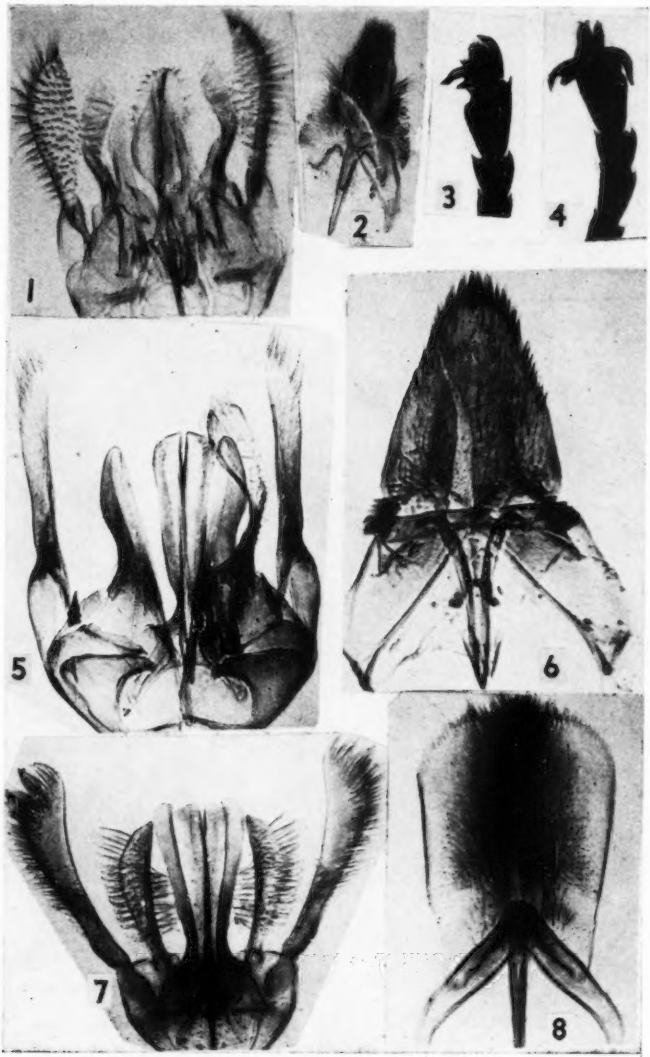
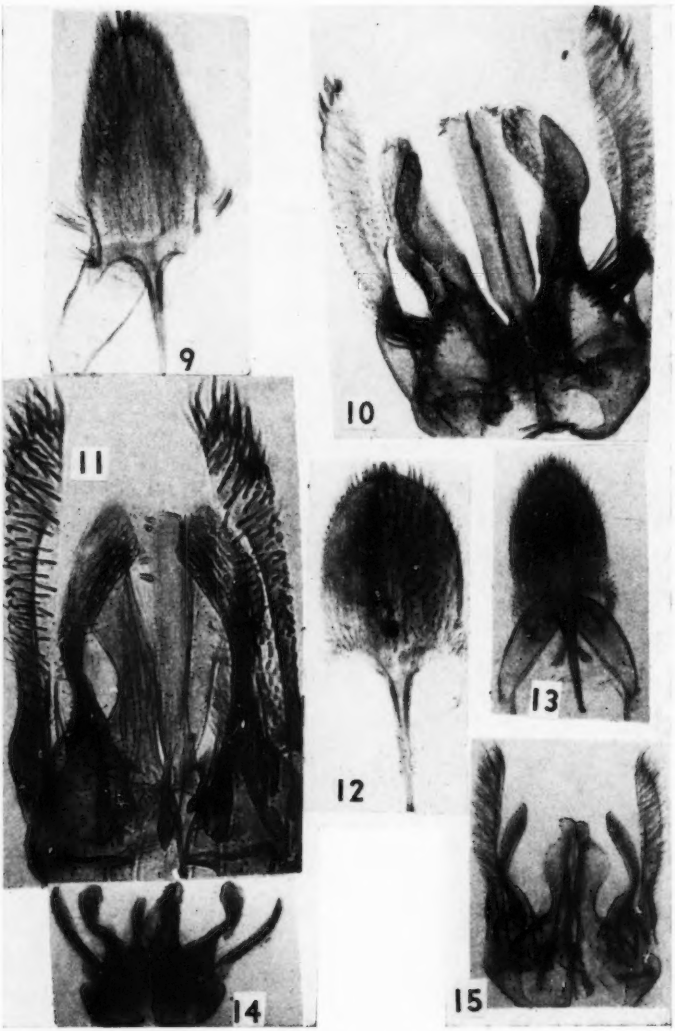
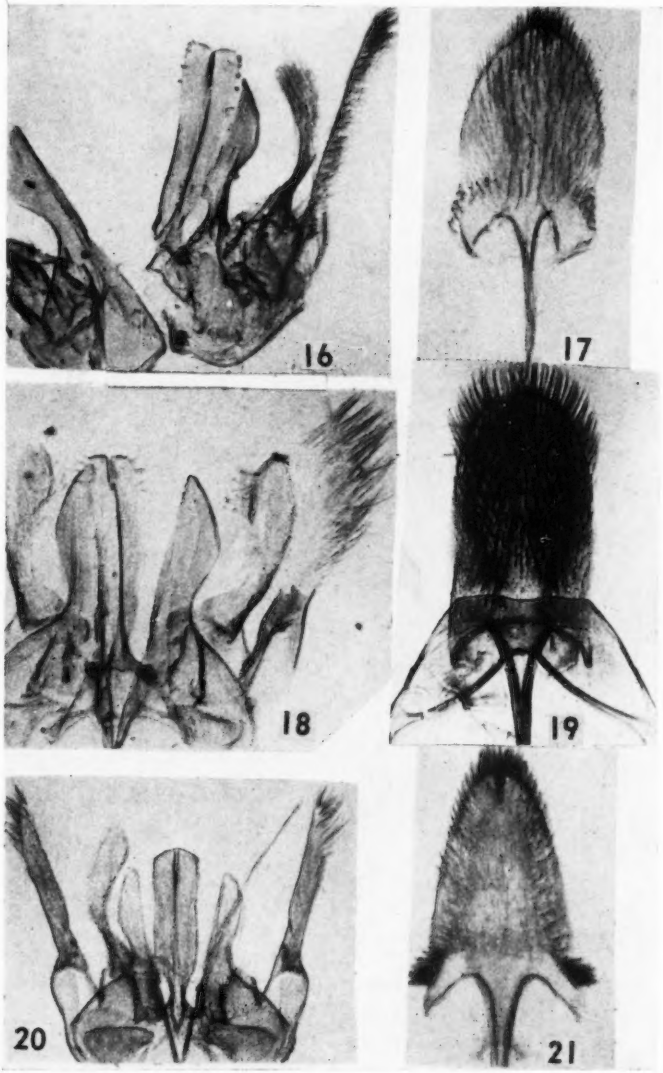
SNODGRASS, R. E. 1941—Smithsonian Misc. Coll. 99, No. 14, Pl. 15.



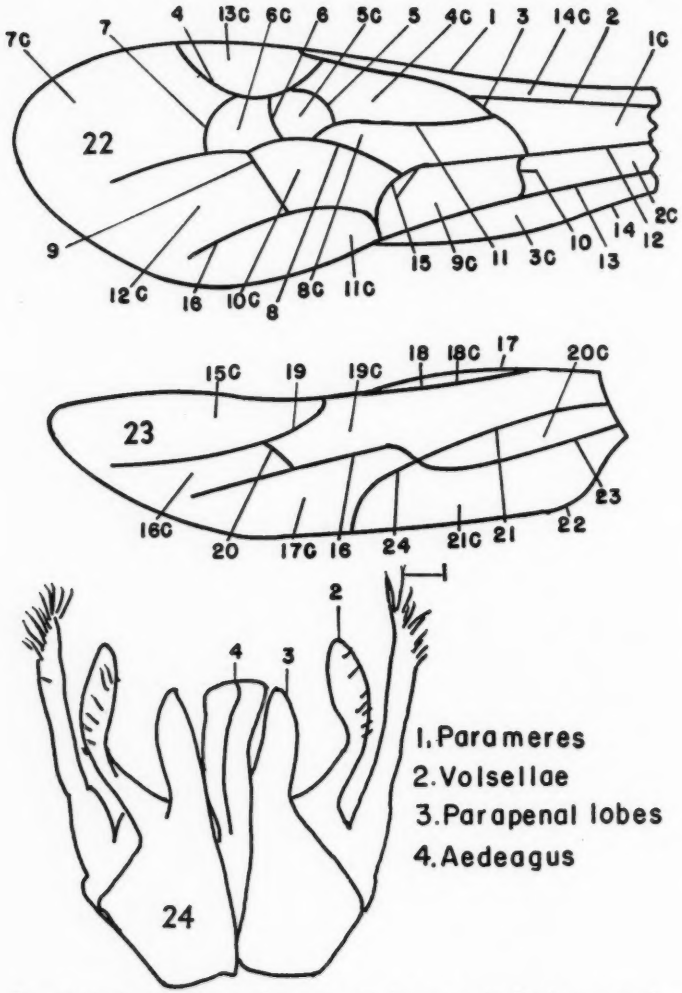
Figs. 1-8.—1. *Anopompilinus anomalus* n. sp., genitalia, ×70; 2. *A. anomalus* n. sp., last ventral segment, ×44; 3. *Pompilinus stenotus* Banks, anterior claw ×55; 4. *P. stenotus*, posterior claw, ×65; 5. *Anopompilinus aspinosus* n. sp., genitalia, ×60; 6. *A. aspinosus* n. sp., last ventral segment, ×60; 7. *Pompilinus stenotus* Banks, genitalia, ×45; 8. *P. stenotus* Banks, last ventral segment, ×48.



Figs. 9-15. *Anopompilinus* spp.—9. *dakota* n. sp., last ventral segmnet, ×65; 10. *dakota* n. sp., genitalia, ×70; 11. *banksi* n. sp., genitalia, ×95; 12. *banksi* n. sp., last ventral segment, ×60; 13. *imbecilla* (Banks), last ventral segment, ×40; 14. *parvulus* Banks, genitalia, ×55; 15. *imbecilla* (Banks), genitalia, ×55.



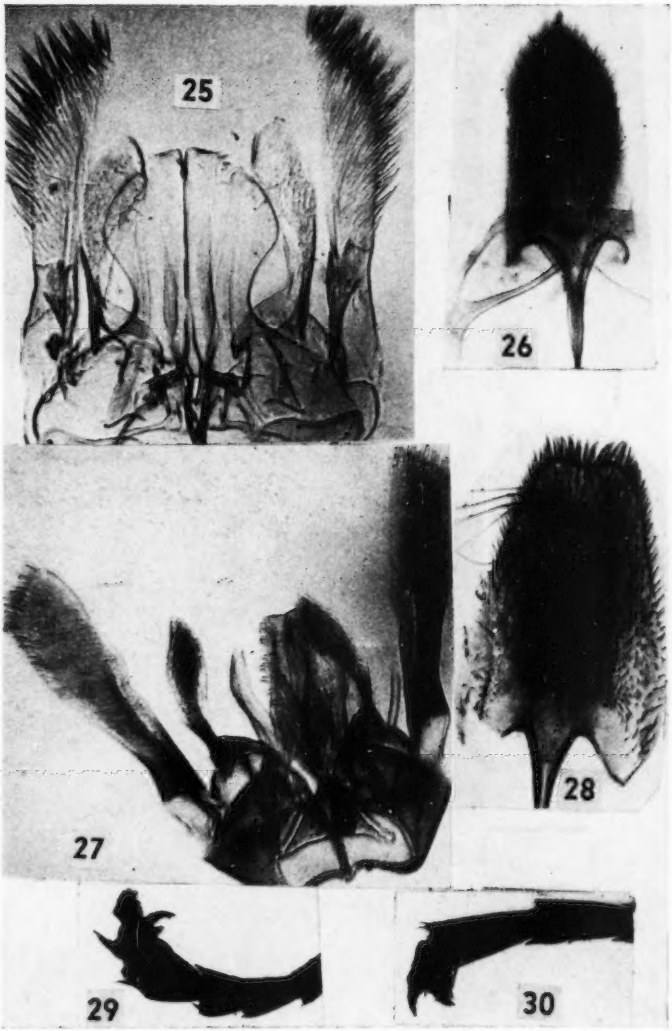
Figs. 16-21. *Anopompilinus* spp.—16. *coloradensis* n. sp., genitalia, ×70; 17. *coloradensis* n. sp., last ventral segment, ×53; 18. *hirsutus* n. sp., genitalia, ×55; 19. *hirsutus* n. sp., last ventral segment, ×65; 20. *michiganensis* n. sp., genitalia, ×60; 21. *michiganensis* n. sp., last ventral segment, ×60.



Figs. 22-24. *Anopompilinus michiganensis*.—22. Fore wing; 23. Hind wing; 24. Genitalia.

Veins.—1. Costal; 2. Subcostal; 3. Basal; 4. marginal or radius; 5. 1st intercubital; 6. 2nd intercubital; 7. 3rd intercubital; 8. 1st recurrent; 9. 2nd recurrent; 10. Transverse median; 11. Cubital; 12. Median; 13. Submedian; 14. Anal; 15. Discoidal; 16. Subdiscoidal; 17. Costal; 18. Subcostal; 19. Radius; 20. Transverse median; 21. Median; 22. Anal; 23. Cubitus; 24. Discoidal.

Cells.—1C. Median; 2C. Submedian; 3C. Anal; 4C. 1st cubital; 5C. 2nd cubital; 6C. 3rd cubital; 7C. 4th cubital; 8C. 1st discoidal; 9C. 2nd discoidal; 10C. 3rd discoidal; 11C. 1st apical; 12C. 2nd apical; 13C. Marginal; 14C. Costal; 15C. Radial; 16C. Cubital; 17C. 1st discoidal; 18C. Costal; 19C. Median; 20C. Submedian; 21C. Anal.



Figs. 25-30. *Anopompilinus* spp.—25. *mainensis* n. sp., genitalia, ×100; 26. *mainensis* n. sp., last ventral segment, ×40; 27. *occidentalis* n. sp., genitalia, ×50; 28. *occidentalis* n. sp., last ventral segment, ×61; 29. *michiganensis* n. sp., anterior claws, ×60; 30. *michiganensis* n. sp., middle claws, ×60.

Observations on Natrix septemvittata (Say) in Southwestern Ohio

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The queen snake, *Natrix septemvittata*, is distributed over a broad range in eastern United States, extending from western New York south to northern Florida, and from western New Jersey west to Wisconsin. In some areas the population is discontinuous, and uncommon where encountered, a situation frequently encountered east of the Appalachian mountains. In other regions the numbers of individuals are large, and the queen snake shows such local abundance in suitable habitat that it becomes the dominant *Natrix* in the area. Southwestern Ohio is particularly favorable as a field laboratory for certain types of observation on *Natrix septemvittata* because of the remarkable local abundance of the species, and the position of the region not far north of the geographic center of the known range.

For purposes of this report the part of southwestern Ohio known as Miami Valley consists of all counties drained in whole or in part by the Great or Little Miami Rivers and their important tributaries, the Mad and Stillwater Rivers. My observations, made in Miami Valley, were made in an intensively cultivated, formerly forested region, a part of the glaciated till plains of Ohio. Drastic changes in the character of the streams due to the erosion of soil, change in water run-off, and change in water temperature resulting from the absence of forest do not appear to have had an unfavorable effect on the *Natrix septemvittata* population.

I have observed this species on many field trips from 1940 through 1947, and have examined over 1,000 specimens. Due to the troglodytic behavior of *Natrix septemvittata* during much of its active season few field observations of behavior are recorded here.

Distribution.—Although Conant (1938a) demonstrated the wide distribution of *Natrix septemvittata* in Miami Valley, the species has not been recorded as present in one-fourth of the counties. Duellman (1947) reported the queen snake in Logan County, and the following records verify its presence in all of the remaining counties excepting Mercer, where no field work has been carried on.

County	Locality	Date	Collector
Clark	Mad River, near Springfield	6-25-40	J. H. Martin
Darke	Greenville Creek, 5 miles west of Greenville	9-8-46	J. T. Wood
Miami	Ludlow Falls, near West Milton	8-4-46	D. E. Ladd H. J. Walter
Miami	Stillwater River, 1.2 miles north of Montgomery County line	8-4 46	D. E. Ladd
Warren	Little Miami River, near Fort Ancient State Park	5-30-42	J. T. Wood
Warren	1 mile west of Waynesville	9-22-46	W. E. Duellman

Habitat.—In Miami Valley, field work indicates *Natrix septemvittata* to be less widely distributed than *Natrix s. sipedon,* but in many areas where both species are found the former has much greater abundance. Conant (1938a) reported this condition prevailed in parts of eastern and southern Ohio. If natural enemies do not operate selectively on these species, and replacement rates are adequate, differences in abundance and distribution are correlated with differences in habitat requirements. Rate of water flow does not appear to have a direct bearing on distribution, but three conditions do appear to be necessary if an area is to support an intense queen snake population, as follows:

1. A permanent water area, either running or still, in which the water remains at or above 65 degrees Fahrenheit during most of the active season of *Natrix septemvittata;*
2. An abundance of cover, usually in the form of flat rocks lying partly in the water, partly on the bank; and
3. An abundance of crayfish (genus *Cambarus*).

Cascades Brook, a tributary of Yellow Springs Creek in Greene County, is an example of an unfavorable habitat. This brook is divided into two drastically different habitats. The upper drainage flows through open farmland is exposed to full sunlight and has little cover since most rocks are too small to conceal a snake. Crayfish are frequently observed, but *Natrix septemvittata* is uncommon due to insufficient cover. The lower drainage cuts through a limestone outcropping in Glen Helen, and consists of a series of connected pools in a wooded area. The forest greatly diminishes the warming effect of sunlight on the water, and additional water enters the brook from seepages below the limestone outcropping. This water maintains a temperature of about 55 degrees throughout the year, and keeps the brook temperature too low for *Natrix septemvittata* during most of its active season. Crayfish are abundant, as demonstrated by the collecting of 300 in a minnow seine in less than 4 hours, and cover is abundant and excellent. The author released 2 dozen marked queen snakes in the lower area of this brook in 1944, but none were recovered. Apparently queen snakes don't utilize this habitat due to unsuitable water temperatures.

Conant (1938a) reported that queen snakes prefer slow-moving or shallow rocky streams but also occur around ponds, lakes, abandoned canals, and less often, perhaps, along the major rivers of the state of Ohio. This is also true of southwestern Ohio with the single exception of major rivers, which often support heavy populations when habitat is suitable. North of Rock Creek, on the west bank of the Stillwater River just below the Englewood Dam spillway, is a habitat that has been worked for eight years on at least 12 field trips. From 20 to 50 specimens have been obtained on every trip, usually in less than an hour's collecting.

Habits.—In Miami Valley *Natrix septemvittata* certainly cannot be "seen at any hour, day or night, from early March until October, hanging from the roots or old trees and low branches—" as reported by Kelly, Davis, and Robertson (1936) from Maryland. In early spring and late fall queen snakes, other than juveniles, are often seen during warm daylight hours sunning on

roots and twigs overhanging the water. In the hot summer months all specimens are found beneath rocks, or in the water. Few specimens have been observed at night in any season, although field work on amphibians has often taken the author into heavily populated *Natrix septemvittata* habitat.

Specimens of queen snake have been seen swimming both on the surface, and less commonly, along the bottom of streams. It is often uncertain that this is not the behavior of snakes disturbed by the observer. "Foraging", as reported by Raney and Roecker (1947), has never been confirmed in Miami Valley. It is not evident that the activity of the snake is a desire for food. Evidence will be presented in the remarks on feeding to suggest that the food comes to the queen snake, rather than that the queen snake goes to the food.

Queen snakes usually do not bite when collected, though specimens longer than two feet may do so, but they actively writhe and twist, and often exude a strong-odored secretion from their cloacal glands. If juveniles are held near the end of the tail they sometimes rotate the body, severing the tip of the tail and giving the specimen a chance to escape capture.

Queen snakes are frequently found under rocks in gregarious gatherings of 3 or 4 specimens, and in one instance 24 were taken from beneath the same rock. They are also found under rocks in the company of other herpetofauna, including *Natrix s. sipedon, Rana clamitans, Rana pipiens, Desmognathus f. fuscus, Eurycea b. bislineata,* and *Eurycea l. longicauda.* Invertebrates found under rocks with queen snakes include spiders, insect larvae, leeches, earthworms, and crayfiish. Of all these animals only crayfish serve as a common item in the diet of the queen snake.

Aggregations.—On meager evidence Conana (1938b) reported that *Natrix septemvittata* showed little seasonal fluctuation in abundance in Lucas County, Ohio. In southwestern Ohio the yield of specimens on a collecting trip is much greater in spring and fall than during the summer months. The author doubts that this indicates seasonal fluctuation in abundance, being essentially an index to the availability of the snakes to the collector rather than an evidence of varying numbers.

In 1944 I reported on aggregation of *Natrix septemvittata,* prior to hibernation, involving 47 specimens. A more striking aggregation was encountered by W. E. Duellman, D. E. Ladd, and R. E. Reicken in White Oak Creek at a point 8 miles north of Georgetown, Brown County. In this instance 125 *Natrix septemvittata* were collected in a shallow, rocky creek, in a distance of 100 yards, in less than 1 hour. As many as 24 specimens were collected at one time from beneath a single rock. This field work was in fall, on September 22, 1946, and appears to be another instance of an aggregation prior to hibernation.

Food preferences.—Crayfish comprise the important food item for *Natrix septemvittata.* Other items occasionally recorded as part of the diet are insignificant in importance. Raney and Roecker (1947) present excellent evidence

of this. In 59 stomach dissections by W. E. Duellman, the 6 containing food contained crayfish. The author recorded 43 disgorgings in the field, and with a single exception noted only crayfish. Pope (1944) Schmidt and Davis (1941), and McCauley (1945) also indicate the importance of crayfish in the diet of queen snakes.

The author observed a large female *Natrix septemvittata* disgorge a 5-inch catfish on June 18, 1940, at Englewood Dam, Montgomery County. Conant (1938a) reported "queen snakes disgorged crayfish and small fish when captured." In response to inquiry he states that he had observed the disgorging of fish on one occasion only, from an individual that also disgorged one or two crayfish. There appear to be no other valid records of fish-eating by this species. The toad has been reported as an item of diet, in a single instance, by Surface (1906). This departure from the usual feeding habit has not been noted in southwestern Ohio.

The current impression that frogs and toads were important in the diet of queen snakes resulted from Ditmar's misuse (1935, 1946) of a qualified guess by C. S. Brimley. Trapido (1937) exposed his inexperience with the species by remarking that the food preferences of queen snakes and common water snakes were similar. Kelly, Robertson, and Davis (1936) also supply data on the food preferences of queen snakes, without the benefit of facts, and substantiate their errors with a faked photograph of a queen snake eating an earthworm!

In southwestern Ohio *Natrix septemvittata* and *Natrix s. sipedon* have distinctly different food preferences, and do not enter into competition with each other in this respect. The distribution and abundance of the two species is probably more directly correlated with the distribution and availability of food supply than with any other single factor.

Feeding.—Field observations on feeding of *Natrix septemvittata* are rare. I observed an adult female queen snake feeding on a dead crayfish on August 16, 1940, in Rock Creek near Englewood Dam spillway, Montgomery County. Rock Creek is a small, polluted stream passing over ledges of fossiliferous shale in a small ravine near the Stillwater River. Several dead crayfish were observed in the immediate vicinity of the queen snake, and the faded coloration and inactivity of the specimen being engulfed indicated it had been dead at least a day. The queen snake swallowed the crayfish starting with the telson, and it proceeded to the base of the great claws when something disturbed it. The snake started to retreat into a crevice in the rock outcropping, and was captured. The dead crayfish was promptly disgorged. Three other queen snakes collected in this same habitat at the same time also disgorged crayfish in various states of digestion. Under natural conditions the queen snake, like the common water snake, will feed on carrion.

Minton (1944) reported queen snakes feeding on minnows, but in response to inquiry, states that the identity of the snake involved had not been determined by examination. Since both queen snakes and common water snakes are

known to occur in the brook near St. Paul, Indiana, where the observations were made, there remains doubt as to which species was observed.

Raney and Roecker (1947) reported "despite its small mouth, the queen snake often catches and eats very large crayfish." The examination of stomachs proves queen snakes eat very large crayfish, but not that they can catch them. It would be most remarkable if a queen snake could catch a large, active, well-armed crayfish, and swallow it alive without being somewhat mutilated in the process. Yet evidence of this, in the nature of missing eyes, scarred heads and necks, and other wounds are rare on queen snakes encountered in the field. If the crayfish were helpless, swallowing would be less of a feat. Crayfish are helpless when they are in ecdysis, and when they are dead.

Since natural death is rarer than ecdysis, it is probable that most large crayfish are eaten in the latter state. No disgorged crayfish observed by the author have been alive, and few have had hard exoskeletons. These occurences seem more than coincidence. Crayfish, when about to shed, retreat under such a rock as would provide shelter for the queen snake, and actually eliminate the need for any search for food, or art in catching it. No evidence exists to suggest that feeding of the queen snakes, based on the intermittent intervals when ecdysis in *Cambarus* is common, would be insufficient to support a large population.

McCauley (1945) dissected a queen snake and found a crayfish and the head of an ant in the stomach. He reported "the latter probably from the stomach contents of some frog or fish which had served as food." On extremely rare occasions fish and frogs are known to serve as food for queen snakes, but it would be extraordinary if the ant could survive the digestive juices of the fish or frog, and those of the queen snake, while all trace of the intermediate predator were digested away. More likely the ant was scavenging in a dead crayfish, and was accidentally engulfed with the crustacean.

Conant (1938a) reported captive *Natrix septemvittata* fed rarely, and then on small crayfish. It is probable that small crayfish, if caught, can be swallowed in any state.

Natural enemies.—On October 20, 1940, a dead queen snake was found on the banks of the Miami River about 10 miles north of Dayton. The specimen was found in natural position beneath a sheet of roofing tin which was partially imbedded in the mud. Mice had gnawed away the flesh on each side of the backbone, and appear to have caused the death. Apparently cold weather had immobilized the snake and rendered it defenseless. I assume this to be an exceptional occurrence.

Reproduction.—Pope (1944) reported the size of 6 broods and dissections of 8 gravid queen snakes, and found an average of 9 young produced at one time. Other records in the literature, plus 4 new ones from Miami Valley, are compiled below. Range in normal brood size is from 5 to 23 young.

Locality	Date	Number of Embryos or Young	Observer
Nelson Co., Virginia	8-31-14	5	E. R. Dunn (1915)
Washington Co., Md.	7-5-36	8	R. H. McCauley (1945)
Baltimore City, Md.	8-7-37	14	R. H. McCauley (1945)
Lucas Co., Ohio	8-18-30	11	R. Conant (1938a)
Clermont Co., Ohio	8-20-32	10	R. Conant (1938a)
Defiance Co., Ohio	6-18-46	23	C. A. Triplehorn (1949)
Montgomery Co., Ohio	8-4-46	11	W. E. Duellman
Montgomery Co., Ohio	10-5-46	10	J. T. Wood
Montgomery Co., Ohio	7-6-40	17	Mario de Jesu
Montgomery Co., Ohio	8-10-46	12	J. T. Wood

By combining Pope's 14 records with the above data, average brood size is 11 young, with larger broods found in larger females.

Variations in a litter.—On August 10, 1946, a 606 mm. gravid female *Natrix septemvittata* was collected in Montgomery County, Ohio, by H. J. Walter. After brief captivity a brood of 12 specimens was delivered. This brood was preserved and studied for variations in scutellation and proportions. No attempt at sexing was made. Total lengths ranged from 175 to 201 mm., averaging 187 mm. Tail lengths ranged from 43 to 51 mm., averaging 48 mm. Klauber (1943) demonstrates that the tail/total length proportion shows ontogenetic variability in some snake species, but this was not found in *Natrix septemvittata*. Tail/total proportion averaged 25.6.

Ventral scutellation ranged from 137 to 146, averaged 142; subcaudals ranged from 65 to 78, averaged 71. These variations are as broad as those noted in an unselected series of adults from Miami Valley.

ACKNOWLEDGEMENTS

The author wishes to acknowledge his thanks to the many field workers who have assisted him in obtaining data on *Natrix septemvittata*, including J. H. Martin, H. J. Walter, M. E. Fitzmaurice, Alfred Verwyst, D. E. Ladd, and R. E. Reicken. Special thanks are due to Roger Conant, Sherman Minton, Jr., and W. E. Duellman for responses to inquiries on particular problems of interest in this report.

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The Molting and Fur Growth Pattern in the Adult Mink

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Pelage changes occurring in various species of the family Mustelidae have been described for the ferret and fitch (Bissonnette, 1935), the mink (Bissonnette and Wilson, 1939) and the weasel (Bissonnette and Bailey, 1944). The descriptions are general in nature and make no attempt to break the molt pattern of these species into definite stages.

When studies are made to determine the possible effect of altered day length upon molt and fur growth it is very desirable to break down the entire molting process into distinct steps which are precisely defined, if comparisons are to be made between different experimental groups. This procedure has been followed for the adult silver fox (Bassett and Llewellyn, 1948). When the molting process is thus broken down it is possible to compare the step by step progress of different groups in a quantitative manner.

Materials and Methods

Twenty adult mink (six females and four males in 1946, and five females and five males in 1947) selected by chance from animals formerly included in the station breeding herd were examined at weekly intervals from May 5 to pelting to determine the character and extent of visible changes taking place in the shedding of old and the growth of new fur. As was true with similar studies on the adult fox, the changes that occurred during the molting cycle of the adult mink were gradual and each step merged imperceptibly into the next.

The adult fox under normal conditions grows only one coat of fur a year, whereas the mink grows two. Furthermore, the two coats of the mink differ in length, density and color, so that fur experts, and even those with little skill in the selection and grading of mink skins, can pick out a "summer pelt" which is worth very little when compared with the winter skin.

Some of the stages in the molting pattern can be easily determined by examination of the mink in its pen or in a mink catching cage, particularly if the fur of the animal is of reddish cast, for as the new hair, which is dark in color, appears the contrast between the old and new hair is very decided. Close examination is required to determine the length of the growing guard hair,

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which is well hidden in the old underfur in its early stages, or the color of the skin, the criterion of primeness. In such cases the mink must be caught and restrained.

As the molting cycle advanced, a description was written of the changes that occurred and the approximate time of year that each stage could be expected to appear. After the written description of each stage had been completed it was compared with the appearance of several other adult mink just entering the same stage of molt. The drawings shown on plate 1 were made on the basis of the written description.

Adult mink at the station are usually completely prime between November 20 and December 1. As the winter progresses the melanin, or guard hair pigment, loses its depth of color and the pelt fades from an extra dark or dark to a dark brown or brown color, although such fading can be delayed to a considerable extent by the selection of breeding animals that have demonstrated their ability to "hold their color." The luster of the guard hair decreases until by late winter or early spring the fur is dull in appearance. This is a general description of mink pelage in mid-April just before the spring molt begins.

STAGES IN THE MOLT AND FUR GROWTH PATTERN OF THE ADULT MINK

Stage 1.—The first indication of winter coat molt is a small amount of dark new hair, barely visible as a black smudge back of the muzzle in the region of the vibrissae (whiskers).

Stage 2.—A small dark ring of new hair, approximately 1/32 inch in width, may be observed around each eye. Additional new hairs, dark in color, appear on the muzzle. These first two stages appear between April 15 and 30 in the Saratoga Springs area.

Stage 3.—The dark ring around the eyes has increased in width to 1/4 inch. The nose, except for the bridge which is covered with old hair, is well darkened, and a smudged appearance is noticeable on the sides of the muzzle from the vibrissae toward the eyes. Generally observed in late April and the first week in May.

Stage 4.—The face from the eyes to the muzzle is dark with new hair, as are the front and hind feet where new growth is just becoming apparent. This stage is generally reached from the 7th to the 14th of May.

Stage 5.—By May 25 the line of new hair extends posteriorly from the eyes to a point on the forehead parallel with the ears. The cheeks are unchanged.

Stage 6.—The area of new hair growth now extends beyond the ears and part way down the back of the neck. Old hair on the cheeks may or may not be shed, but that on the sides of the neck still adheres. Some loose hair is becoming apparent on the body. The stage is observed the last of May and the first of June.

Stage 7.—By the middle of June the cheeks and underside of the neck to

the shoulders are covered with dark new hair. The front legs are beginning to darken as new growth extends dorsally. Some new hairs may appear in the shoulders. The hind legs have darkened and new growth stretches to the buttocks and the base of the tail. A streak of new hair extends ventrally from the throat to the groin. Old hair of the body is dull in appearance.

Stage 8.—Between the middle and the end of June this stage arrives. The shedding of old hair all over the body is well started. The shoulders and hips are dark. The sides and flanks still retain the old fur. The tail is fully furred. Old guard hair is present but in decreasing quantities, and most of the pelt is assuming a darker shade.

Stage 9.—Few old hairs are visible on the body. Growth of the summer coat is nearing completion by early July.

Stage 10.—Shedding of the winter coat and growth of the summer pelt are completed by July 15 to 20. The pelt is prime but instead of the light cream skin color which is associated with the winter prime pelt, the color is a much deeper yellow.—Fur color is lighter and not so intense, and fur density is not so great as in the winter pelage. Nevertheless the coat is sleek and dark in appearance.

Stage 11.—The sleek, shiny summer coat of the adult mink is retained for a period of about three weeks, from mid-July until early August, and then a dusty appearance gradually becomes noticeable. The guard hair and underfur, when pulled sharply, come out in approximately equal proportions. The skin of the tail tip develops a bluish tint. Shedding of the summer coat and growth of the winter pelage have started.

Stage 12.—When pulled firmly but not sharply, hair on the sides and back comes out easily. The underfur is far more plentiful in the plucked hair than is the guard hair. The skin is a light pinkish blue except at the tip of the tail where it may sometimes be blue. This stage extends from late July until about August 20.

Stage 13.—About September 1, new guard hair, about 1/8 inch long, can be found among the old underfur on the posterior third to half of the tail. The color of the skin of the tail varies from a light blue near the body to a dark slate at the tip.

Stage 14.—Fur of the summer coat pulls out easily but there is still no evidence of general shedding. The skin of the body is a light pinkish blue; that of the tail a dark slate. The posterior third of the tail is dark in color, sleek in appearance and well furred. New fur growth which is tight and hard to pull out is evident on the posterior two-thirds of the tail. This stage is usually completed by mid-September.

Stage 15.—By the last of September the tail is fully furred. The skin at the tip of the tail is light blue in color, while near the base of the tail and on the body it is a darker color. The old fur is dusty and dull. There are many loose hairs and much scurf on the body.

Stage 16.—Stages 16 to 20 occur much more rapidly than the other stages previously described. The time consumed in completing the next five stages requires only 6 to 7 weeks.

Skin of both the body and the tail is light blue in color. The fur is still somewhat dusty. New guard hairs about 1/8 inch long can be seen on the hips and sides if the old underfur on these areas is examined closely. This stage is generally observed from October 1 to 10.

Stage 17.—Between October 14 and 21 careful examination will show new guard hairs 3/8 inch long on the hips, sides and back. Underfur growth is becoming evident in these areas. The roots and shafts of the new hairs are jet black in color. New guard hair is appearing on the shoulders, neck and head, although the old underfur on these areas must be examined closely to find it.

Stage 18.—From October 21 to November 10, both stages 18 and 19 are likely to have appeared. In stage 18 the new guard hairs are 1/2 to 5/8 inch in length. The old guard hair present pulls out easily. The animal is still dusty in appearance and numerous loose hairs are scattered over the body. Shedding of the summer pelage progresses anteriorly from the tip of the tail toward the muzzle, which is the opposite direction followed in the shedding of the winter coat.

Stage 19.—The guard hairs are now about 3/4 inch in length. If some of these hairs are pulled out it will be observed that the roots are still dark although the proximal portion of the hair shaft is lighter than when previous observations were made. The animal is still dusty in appearance, especially on the head and neck. The skin color of the tail, hips, flanks and back is very slightly blue, but the head, neck and shoulders are somewhat darker.

Stage 20.—Dustiness of the pelt has completely disappeared. The skin is a light cream or creamy white in color. The pelage is dark and glossy in appearance. The animal is completely prime. This stage is generally reached between November 12 and 25 in the latitude of Saratoga Springs, N. Y. One of the animals of this study was prime on October 28, whereas another was not ready for pelting until November 25.

DISCUSSION

Observations were made in 1945, 1946 and 1947 to determine the molting pattern of adult mink. It was observed that there was considerable variation among both individuals and groups in different years, even when they were maintained under approximately the same conditions. One male (D331) reached stage 13 on July 22 and had not advanced to stage 14 until September 16. Mink E314 passed from stage 12 into stage 14 in the two weeks from August 19 to September 3. It would seem necessary, therefore, to include a control group in any future experiments involving the molting pattern or pelage change in adult mink.

Table 1 gives the weekly record of observations made on the ten animals

studied in 1946, and another ten studied in 1947. Figures given are group averages.

If individual variations are disregarded, there is no significant difference between the sexes in the molting pattern followed or in the time required to complete the different stages.

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TABLE 1.—Observations on the molting and fur growth pattern of adult mink.

Year 1946; 6 females, 4 males		Year 1947; 5 females, 5 males	
Date	Molting stage	Date	Molting stage
May 27	6.2	—	—
Jun. 3	7.2	Jun. 2	6.0
—	—	Jun. 9	6.8
Jun. 13	9.2	Jun. 16	7.0
Jun. 21	9.6	Jun. 22	7.8
Jul. 1	9.9	Jun. 30	8.2
Jul. 8	10.5	Jul. 9	8.2
Jul. 15	10.5	Jul. 14	9.0
Jul. 22	11.9	Jul. 22	9.8
Jul. 29	12.0	Jul. 28	10.8
Aug. 5	12.0	Aug. 5	12.1
Aug. 12	12.1	Aug. 11	12.2
Aug. 19	12.3	Aug. 19	12.9
Aug. 26	12.8	Aug. 26	13.0
Sep. 3	13.2	Sep. 3	13.6
Sep. 9	13.2	Sep. 9	13.7
Sep. 16	14.3	Sep. 16	14.3
Sep. 23	14.9	Sep. 23	14.5
Sep. 30	15.1	Sep. 30	15.1
Oct. 7	15.9	Oct. 7	15.5
Oct. 14	16.3	Oct. 14	16.1
—	—	Oct. 21	17.1
Oct. 28	18.7	Oct. 28	17.7
Nov. 4	19.3	Nov. 5	18.4
Nov. 12	19.8	Nov. 10	18.5
Nov. 18	19.8	—	—
Nov. 25	20.0	Nov. 25	20.0

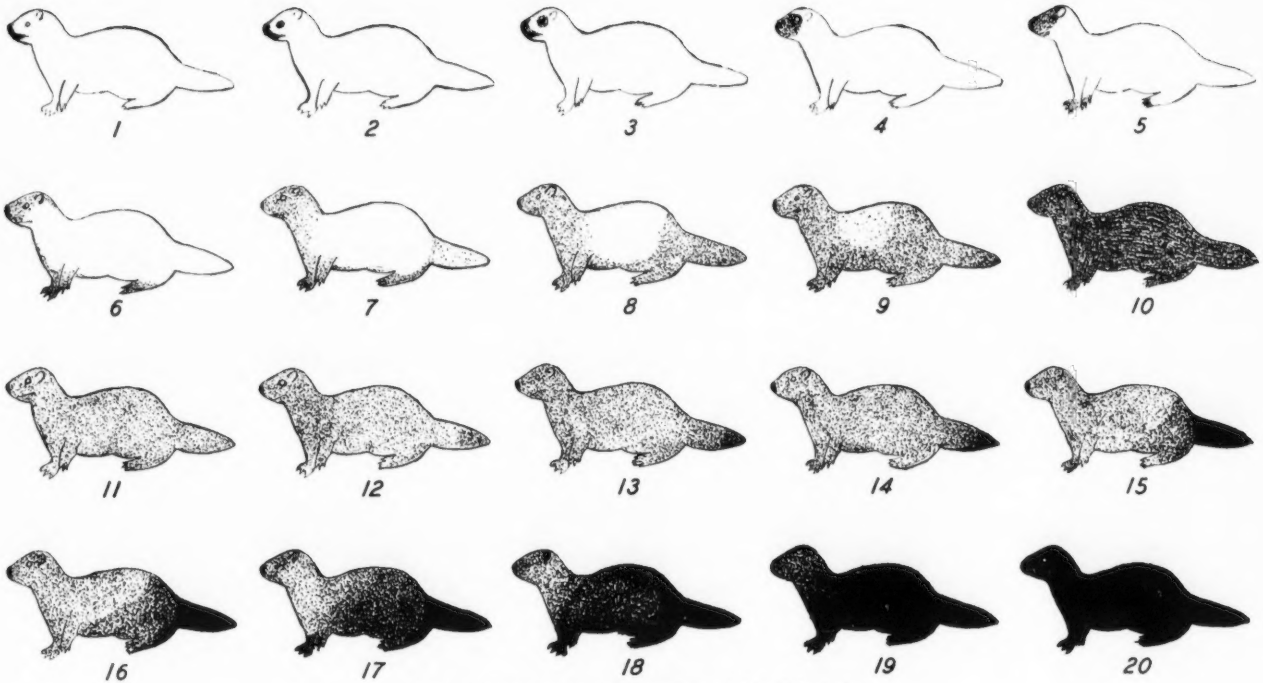

Fig. 1.—Stages in the molting pattern of the adult mink.

Notes and Discussion

Reduction of the Time Factor in Rearing Australorbis glabratus*

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In any investigation involving digenetic trematodes, the biology of the snail intermediate host must be considered. Anything which affects the well-being or the life cycle of the snail may be of value, and in keeping with this thought the following observations are recorded.

Simultaneously aquaria were inoculated with a wild culture of green algae predominantly of the genus *Oscillatoria*. This wild culture was nourished with a hamster manure-and urine crude extract made by boiling 500 grams of faeces-urine mixture in one liter of water for one-half hour and filtering off the liquid for use. On alternate days 5 cc. of this extract were poured into the inoculated aquaria and in two weeks time the sides of the containers were covered with the green algal growth.

Australorbis glabratus, the intermediate host of *Schistosoma mansoni*, was established in an unbalanced aquarium as a "stock" culture of snails and was fed on lettuce only. On the day these snails oviposited, the ova were transferred to a small culture dish of filtered river water and 13 days later they hatched. Some of the young were immediately transferred to one of the aquaria containing *Oscillatoria* while others of the hatch were placed in a filtered river water culture and were supplied with finely chopped lettuce.

The young snails fed avidly on the algae and grew more rapidly than did those allowed to feed on lettuce only, so that the former matured and oviposited in 63 days, 17 days earlier than the young lettuce-fed snails. This speeding up of the life cycle through feeding has a direct bearing on the ease with which experimental work on Schistosomiasis mansoni can be carried on in the laboratory in that less time and fewer snail cultures are involved in continuous experimentation.

It was incidentally observed that when the pH of the aquaria exceeded 7.8, oviposition was slowed and at a pH of 8.2 it ceased altogether. Oviposition was resumed when the pH was returned to 7.2. Decomposition of organic material (leaves, stems, mud, etc.) in other aquaria, with attendant release of gases, did not produce a medium below pH 6.8 and although the decomposing organic debris periodically rose to the surface and then in a few days fell to the bottom of the aquaria**, snails prospered throughout the decomposition process. The periodic rising of the organic debris was apparently due in large part to the release of oxygen from algae.

Inch long pieces of common blackboard chalk, used to provide calcium for the snails and to maintain the pH of the aquaria at near neutrality (McMullen, Amer. J. Hyg. 45(3) 1947), were added whenever a layer of protozoan ciliates appeared. At first the layer appeared as a faint cloudiness about one inch from the bottom of the aquarium but

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* This work was made possible through the courtesy of Dr. Michel Piljoan of the Chemical Foundation of Colorado at Boulder, who supplied the snails for research purposes.

** Personal communication with Drs. Elder and Campbell of the University of Missouri pointed out this same occurrence in natural waters.

gradually moved upward and became more dense as the pH changed. The protozoa proved to be a fairly reliable guide for need for adjusting the pH of the aquaria.

Snails without chalk sticks in their aquarium had deeply etched shells which did not exceed one centimeter at their greatest width. When some of these same snails were moved to an aquarium to which chalk was periodically added they resumed growth which left a ridge where new shell was added and the new shell was not eroded. Other snails reared from eggs and always supplied with an adequate amount of chalk, had somewhat irridescent shells of a light brown color and the shells were semi-transparent. No erosion was seen and the snails attained a diameter of 1.5 cm.

Additional records* made in a different area where the water has a high degree of hardness show that chalk is unnecessary for rapid growth and perfect shell formation. Apparently the snails are able to extract sufficient salts from local water for their requirements.

In one culture it took 6 days for ova to hatch and in this lot of snails there was a growth of 5 mm. in diameter during their fourth week. When these snails reached 11 mm. in diameter, 36 days after hatching, they oviposited. This represents the second substantial reduction in the time required for completion of the life cycle.

By continuation of observations and refinement of methods it is hoped that a more exact ecology can be established for these foreign snails.

* Records from the Department of Zoology, University of Missouri, Columbia.

Corallorrhiza maculata Raf., A New Distribution Record

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Two specimens of *Corallorrhiza maculata* Raf., were collected by the authors in Warren Woods (Berrien Co., Mich.) on July 15, 1949. Both plants which were not quite fully mature and grew in deep humus in a grove of large beeches, were almost completely covered by a thick layer of decaying leaves. This species, apparently unreported in this particular locality, is fairly common in neighboring northwestern Indiana and southwestern Michigan.

No. 213594, Nieuwland Herbarium, Univ. Notre Dame, Notre Dame, Ind.

Book Reviews

GILLMAN'S TANGANYIKA VEGETATION MAP. By Clement Gillman. A vegetation-types map of Tanganyika Territory. Geogr. Rev. 39(1): 7-37. 1949. 32 figs. Colored 1:2,000,000 map. Reprints for sale by Amer. Geogr. Soc., N. Y. 32, N. Y., $1.00.

It is not often that students of vegetation receive such an imposing and definitive contribution to their literature as that of this vegetation reconnaissance of Tanganyika Territory. The work is based on the fieldbooks and travel diaries of Clement Gillman, outstanding geographer of east Africa, accumulated from 1913 to the very moment of his death in 1946, and representing some 27,500 km. of travel routes, much of which was checked several times. The considerable burden of compilation and organization of data rested with the editorial staff, whose 1500 hours of working time involved in the preparation of the drafts for a 1:500,000 preliminary map and of the 1:2,000,000 reduction are permanently monumented in the map accompanying this publication.

The classification of vegetation and the map built thereon are strictly physiognomic. Eight main types are recognized, using a nomenclature which avoids: (a) tautologies such as "evergreen rain forest"; (b) importations possibly not suitable such as "steppe" and "veld"; and (c) vernacular terms such as *miombo* and *nyika*. Although these standards are definitely on the conservative side, it is all the easier for future investigators to evaluate the vegetation for any treatment including a larger part of Africa. The eight types are as follows: 1. *Forest* is a continuous stand of trees, either evergreen or deciduous, occurring in lowlands, uplands, swamps, river borders and coastal saline marshes. 2. *Woodland* is an open cover of trees, leafless for some period of the year, with grasses and herbs as the ground cover. 3. *Bushland and thicket* is land carrying more than 50 percent cover of densely growing evergreen or deciduous shrubs or small trees. 4. *Wooded grassland* is land covered with grasses and herbs, with trees and bushes occupying less than 50 percent of the ground. 5. *Grassland* includes Valley Grassland related to seasonal flooding, and Ridge and Slope Grassland on drained uplands. 6. *Permanent swamp vegetation* consists of grasses, reeds and rushes. Swamp forests are classified as Forests. 7. *Desert and semi-desert* is land where the vegetation is absent, or so thinly scattered that the color of the soil dominates the landscape, and occurs on the high cold slopes of Kilimanjaro, and in extremely salty depressions. 8. *Actively induced vegetation* is land so dominantly under the influence of human activities that its vegetation is a complex pattern of crops, pastures, secondary growth and a few relict areas.

A section follows on "Complexes and Catenas," a phrase semantically analogous to "leal and loyal." Catenas (L. chains) are repeated sequences of vegetation types due to regularly alternating conditions of topography, hydrography and/or soils. They are areas of repeated intrazonal types, referred to as alternes and vegetational mosaics by other authors. Three large areas of catenas are discussed. There is a section on "Tectonic Controls" in which is discussed the geologically recent shattering of the earth's crust in this part of Africa, with its prominent effects on altitude, topography and rainfall. Although the reader is here advised to follow physiographic and geologic maps in other publications, a text figure would have been much welcomed by the reader of the Geographical Review. Then follows a discussion of the Brachystegia Woodland, which covers nearly one-half of the Territory's land surface. The reader's attention is drawn to the pitifully small area of remaining forest, and the threat to the country's remaining water resources. This author too writes that "The geographer should never tire of pointing out, with all the scientific emphasis at his command, the important interrelations between the small still-forested uplands and the vast foot plains. The plains can remain, or again become, the home of a stable peasantry only if the forests are protected against the rapacious inroads of the mountain dwellers and if their rehabilitation is energetically furthered without delay in the many areas where deterioration is advanced." This view is close to the philosophy which certain soil scientists have recently tried to ballyhoo as "scare talk," with claims that soil is now producing as much or more than it used to, due to improved agricultural techniques.

It is to be regretted for posterity that such myopic individuals cannot separate production data per acre of remaining soil, from production per acre of land after the soil has been washed away. In a final section, the extremely small area of alien, i.e., European, agriculture is contrasted to the much larger area of native agricultural lands, even though this latter occupies a relatively small part of the Territory. Two appendices compare the present map with earlier ones by Engler and by Shantz, and discuss the source materials of this publication. The numerous photos are reproduced on a large scale, and are well chosen to represent the distinctive types of vegetation.

The 1:2,000,000 map accompanying this paper is a model of cartographic excellence, many aspects of which could find more frequent application in botanical publications. The map measures approximately 60 cm. square. There are two inset maps, one showing the distribution of baobab, and another showing the relative reliability of the map, in which one notes that 55 percent of the Territory is considered to be mapped with "high reliability." The color scheme utilizes highly contrasting tones, chosen specifically to bring out prominently those types of restricted and significant distribution. Thus the solid black of the forest remnants, and the bright red of the Alien Induced Vegetation are quickly apparent. The mapped types are numbered in the same sequence as that used in the text, with subdivisions clearly marked as such. This consistency is a blessing to the reader who has struggled with the nomenclatural multiplicity of such a publication as one of those for southern Florida. Where remnants of one vegetation are scattered through an area of another, as forest remnants in grassland, or where forest is beginning to disintegrate by inliers of another type, the situation is quite adequately symbolized by small dots of one type scattered in the area of another type. The three large areas of catenas are well symbolized by pajama-stripes of their component types. The dotting and the striping appear adequately to cover those cases where vegetation types overlap, spatter out, intergrade and interdigitate.

For those botanists interested in the development of vegetational thought, Mr. Gillman's paper has special significance. This study of Tanganyika is a milepost in the utilization of physiognomy for the classification of vegetation. Moreover it follows on the heels of another physiognomic classification proposed for worldwide use (Küchler, A. W. Geogr. Rev. 37: 233-240. 1947) and applied to Manchuria (Ecol. 29: 513-516. 1948). The classifications of these two men are closely allied in their practical application, yet their evaluations of the technique and their philosophical approaches are so extraordinarily divergent and respectively so clearly phrased that these papers have value as permanent expressions of contrasting modes of scientific thought. The distinctive approach of each man is expressed below.

Küchler at first discusses the well recognized confusion that exists today in vegetational terminology. With this we all agree. He then proceeds (as did originally each of the men responsible for that confusion) with "A New Classification Proposed." "The author [Küchler] is happy to acknowledge his inspirational debt to Köppen" and indeed the Küchler classification is a direct take-off on the Köppen technique. There are seven major physiognomic groups, designated by capital letters, and 18 categories designated by lower case letters. Any particular vegetation is designated by a combination of both capital and lower case letters. As examples, 12 vegetations are listed, with a line or two of description. Concerning these seven major groups, "The fundamental geographic division of the plant kingdom is that between woody plants and the non-woody or herbaceous ones." Six of the seven major groups are composed of these woody plants. "The appearance of the . . . [non-woody plants] in the landscape is relatively uniform; they are therefore all combined under . . . one capital letter." This interesting bias might not go unchallenged by one who has lived in and appreciated more than one of the grasslands of the world. Nevertheless, "the classification presented in this paper describes the vegetation of any region with satisfactory detail. It does not give the species that make up this vegetation." Küchler refers to classifications of Du Rietz, Braun-Blanquet, and to papers of several British authors, but he makes no mention of the physiognomic groundwork established by several early 19th-century plant geographers, especially Humboldt, of the physiognomic vegetational work of Raunkiaer and of Vahl, nor of the widely known and contemporary physiognomic system of Rübel, without consideration of which it would seem strange to

set up still another physiognomic system. Presumably Küchler chooses to ignore rather than attack the somewhat axiomatic statement of Braun-Blanquet (Plant Sociology. McGraw-Hill. 1932. P. 361) that "Attempts at a classification of plant communities reach well back into the last century. The changes this classification has suffered remind us of the history of systematic botany. The first grouping was based upon obvious but purely superficial characteristics: physiognomy." On these individualistic grounds, "the author has started work on the great and difficult project of drawing a unified vegetation map of the world," for which "he urgently invites his colleagues everywhere to send him vegetation maps. . . ." The reader should note that this paper was entitled "A geographic system of vegetation," to which there can be no objection except that of possible redundancy, as *any* mapping of world vegetation is *ipso facto* geographic. It is fully acceptable that his physiognomic system is *a* geographic system, i.e., one of many possible geographic systems.

One year later, we find Küchler's first application of his physiognomic technique. "A new vegetation map of Manchuria." "The map is based on the latest method of presenting vegetation: the Geographic System of Vegetation. . . ." The capital letters (itself an unusual editorial practice) and the replacement of "a system" with "the system" are Küchler's. This interesting semantic metamorphosis makes us wonder whether all previous physiognomic treatments are to be relegated to the junk pile with Model T's and hand-cranked telephones, with floristic and all other vegetational taxonomies, and that at last science may have discovered the one and only natural geographic system. I truly hope that this might be so.

To Gillman. Below the author's name on the first page one reads the text "To know what is, is vital for discussing what ought to be." What a refreshing phrase, and how different the science of ecology might have been had others adopted this theme as a motto, and kept it framed over their desks. In introducing the physiognomic classification, we read that they "set out to classify vegetation by vegetation and not by anything else that may or may not be closely correlated with it. In leaving out questions of successional status we classify vegetation not by what it perhaps used to be, nor by what it will become according to some current theory, but by what the surveyor finds." It is my opinion that these two quotations are unique in vegetational literature. They set the stage for this particular treatise, and we read on with an unusual sense of simplicity and freshness. We look forward to knowing what the vegetation really is; we sense the value of the author's very basic and simple classification; we are awed by the vast amount of fundamental data that has been tabulated for the use of future scientists; we admire the self-discipline of the author in refraining from theorizing and interpreting in situations that have tantalizing potentialities. Here is a well written first chapter of a book which others will some day complete; not the last chapter based on assumptions of the contents of the other chapters. Valuable as is Mr. Gillman's permanent contribution to the empirical geography of eastern Africa, posterity may find that the greater contribution was to this aspect of vegetational methodology.—FRANK E. EGLER, Aton Forest, Norfolk, Connecticut.

BIBLIOGRAPHY OF ANIMAL VENOMS. By R. W. Harmon and C. B. Pollard. University of Florida Press, Gainesville. 1948. i-xxx + 1-340. $8.00.

This book, as the name implies, is a bibliography of the literature of venomous animals and their venoms. Snake references predominate. The literature of the period 1875 to 1946 is covered, 4,157 titles being listed.

A foreword by Drs. Lucien Y. Dyrenforth and H. Marshall Taylor points out the increasing importance of venoms in the treatment of disease. In a brief preface the authors state that the bibliography was compiled primarily for use in connection with their own research projects. It is explained that the entries were secured through a survey of ten abstracting journals, including *Chemical Abstracts*, *Biological Abstracts*, and the *Index Medicus*. There follows a key to the periodical abbreviations used in the bibliography, after which comes the bibliography itself, the entries being segregated by years and arranged alphabetically under each year. This, the essential part of the text, occupies 307 pages. Each entry includes a serial number, the name of the author, the title of the paper,

and the reference data—that is, the name of the journal in which it was published, the volume number, and pagination. Also, each entry contains the references in the abstracting journals (often more than one) where the citations to the original publications were found, each such abstract being set off on a separate line. Finally, the book contains an alphabetical index of authors (pp. 309-340) in which the serial numbers of the papers by each author are given. This, of course, is necessary since the main bibliography comprises a series of annual lists, rather than a single alphabetical list.

The book is cloth-bound and is printed in good type on serviceable paper; it should withstand the continuous usage it is sure to receive in the hands of those interested in the subject. For it goes without saying that a bibliography of 4,000 titles on this important subject, of interest alike to biologists, chemists, and physicians, will be a welcome and useful addition to the library of everyone working in any phase of the subject, herpetologists especially.

One may wonder why 1875 was used by the authors as the beginning date of their bibliography. The literature prior to that date was very large; Mitchell (1860) included a bibliography of 306 items and it was by no means an exhaustive one. If any single paper might be selected as initiating a new era in the field it might well be this one by Mitchell, because of the thoroughness with which his experiments were carried on. From another aspect it was Sewall (1887) who instituted a revolution in the treatment of snake bite, for he was the first to prove that repeated sublethal doses of venom would build up an immunity that would permit an animal to withstand what otherwise would be a fatal dose. This antedated the era of antivenin, initiated independently by Phisalix and Bertrand (1894), and by Calmette (1894). Thus the date 1875 was well selected if it was the desire of the authors to begin their list well in advance of the discovery of antivenins.

Whether the chronological type of bibliography selected by the authors is the most efficient, depends on the objective of the user. If his project is historical, then this form is the best for his needs; if, on the other hand, he wishes to find the journal in which A. A. Aaron published a certain paper, or if he wishes to investigate all that Aaron has had to say on cobra venoms, then he must go through the rather cumbersome procedure of writing down the numbers of all the Aaron references found in the author index, after which he must seek them out year by year as long as Aaron continued to publish. Whatever the purpose, I found that running down references was greatly facilitated by placing the appropriate year figures in red at the top of each page. On the whole, it has been my experience that single, all-inclusive bibliographies are more efficient as references than those segregated on a chronological, subject, or geographical basis. Phisalix (1922) and Pawlowsky (1927) have examples of the subject types of bibliography; H. M. Smith (1946) of the geographical arrangement.

One innovation for which the user will be grateful is the translation into English of all the foreign-language titles.

From the number of papers ascribed to each author one may get a rough idea of the extent of their activities; and, from the titles of their papers, the nature of their lines of research. One notes, for example, the recent work of D. I. Macht, R. N. Chopra, and J. S. Chowhan on the therapeutic uses of venoms; of E. Grasset on detoxification in connection with immunization; of B. N. Ghosh and S. S. De on venom composition; of C. H. Kellaway and Marie Phisalix on venom differentiation and effects; and, in fields other than snake venoms (although not restricted to such fields) K. K. Chen, A. L. Chen, and R. Hamet (Raymond-Hamet) on toad venoms; E. Sergent on scorpions; and J. Vellard on spiders.

Most of the entries give complete references by volume and limiting pages. A few, no doubt because of the inadequate entry in the abstracting journal, supply only the first page number, and in a few cases only the date of publication of the original article. It is also to be regretted that the pagination is not given of such complete books as are listed. Limiting pages often give the researcher a useful indication of the scope of the reference.

The most important criticism of this bibliography that may be made has to do with its completeness. In their preface, the authors acknowledge that "some important publications doubtless have escaped our detection," and it may readily be admitted that a complete

bibliography on any subject as broad as this has yet to be compiled. But the relatively small number of abstracting journals consulted, as well as their particular character, has led to definite limitations in this work, with a far better coverage in those fields having chemical and medical aspects than those of a faunal nature. One regrets that the *Zoological Record*, with its subject index, particularly Section XVI, *Amphibia and Reptilia*, was not consulted, especially the subject indexes under "Poisons" and "Morphology," the latter including special headings under "Teeth" and "Glands." *Copeia* and *Herpetologica* would also have been fruitful. Without these sources it could hardly be expected that books and papers primarily on regional faunas, taxonomy, or habits, but containing much of incidental importance on snake bite, would have been included, for they are seldom listed in the medico-chemical abstracts. Their titles rarely divulge the incidental material on venoms that they contain, although this is often more important than many articles devoted exclusively to the subject. Examples among the omissions of this kind are Ewart (1878) and Stejneger (1895). We miss particularly the many well-known texts descriptive of the snake faunas of particular areas, of which Ouwens (1916), Scortecci (1939), Schmidt and Davis (1941), Malcolm Smith (1943), and Loveridge (1945) may be taken as examples. These often contain important discussions of the snake-bite hazards and the morphology of the venom apparatus of the particular snakes found in the territories covered. Among recent papers on snake fangs that have been omitted are those of the present writer on rattlesnake fangs (1939) and Bogert (1943) on cobra fangs. The perfection of the injecting apparatus has an important bearing on the seriousness of snake bites.

Even in the medical field, the coverage would have been more inclusive had the authors consulted the three completed series of the great *Index-Catalogue* of the Library of the Surgeon-General's Office under the heading "Reptiles," "Serpents," and "Venoms," to say nothing of "Fish (poisonous and injurious)," "Scorpions (stings of)," "Spiders (bites of)," and "Toads (venom of)."

But probably the most fruitful sources not utilized by the authors are the bibliographies contained in some of the notable papers of the past, several of which bibliographies have been quite extensive. For example, the work under review contains one reference for 1875, none under 1876, and two for 1877. In contrast, the bibliography of Mitchell and Reichert (1886) contains 19, 15, and 9 items for these respective years. I do not suggest that the proportion of omissions in later years is as high, for the coverage by the abstracting journals has improved, but the omissions are extensive and many of them are of importance in the development of our knowledge of venomous animals and the wounds that they produce.

For example, among the books devoted to the subject I failed to find the following included: Anon (1880), Bieling, et al., (1936), Brazil (1911, 1914), Corkill (1932), Halpern (1936), Noguchi (1909), Picado T. (1931), and Vellard (1944). The Noguchi monograph, with its bibliography of 405 references, is probably the most conspicuous omission of all.

In some cases certain editions of a work are given but not others. For example, the English translation of Calmette's work (1908) is cited but not the original French publication (Calmette, 1907). The first edition of Vincent Richards' book (1885) is listed but not the second (1886).

An important series of works overlooked, comprising a summary of abstracts, not only on snake venoms, but those of other animals as well, is that of Maass (1933a, 1933b, 1937).

But despite these conspicuous and even important omissions, the coverage of the subject is complete enough to comprise a work that will prove one of the most indispensable in the library of any student of venomous animals.

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—L. M. KLAUBER, 233 West Juniper St., San Diego, California.

HUMAN ANCESTRY FROM A GENETICAL POINT OF VIEW. By R. Ruggles Gates. Harvard University Press. 1948. xvi+422 pp., 27 plates, 8 text figures, 23 tables. $7.50.

Darwin was well aware that the weakest part of his theory lay in the complete ignorance which then prevailed (or so he thought) with respect to the processes of heredity. And so it is appropriate that this, the latest book on human evolution, should be written from a genetical point of view. Many will feel, however, that this work is not on a par with the author's *Human Heredity*. The major conclusion of this book is that the principal races of man are in fact good species, their resemblances being based on parallel evolution of several distinct lines, while their differences are based upon non-relationship.

After a brief introduction which indicates this major thesis, Gates discusses the principle of parallel evolution at some length, giving many examples from diverse groups of animals. He then continues with numerous examples of parallel evolution among the mammals specifically, giving the impression that he regards parallelism as one of the most frequent and fundamental of evolutionary phenomena.

Finally, he applies this principle to the interpretation of the evidence bearing on the phylogeny of man, and thus arrives at the conclusion that the major races of man are, and long have been, five distinct species.

Some concern has been expressed over the possibility that the description of the major human races as distinct species may accentuate existing racist controversies and cause new outbreaks of racism. There is nothing in the text which indicates that Gates intended to give aid to advocates of racist doctrines, yet there is no doubt that the main thesis of this book could be so perverted by demagogues. This raises the very important question as to whether a scientist should withhold from publication what he believes to be the truth, when he knows that it may be used for evil ends. The reviewer can hardly claim to answer this difficult question, but believes that the value of scientific truth as such should be given full weight before judging the author adversely.

Gates has assembled a vast amount of previously scattered data both on physical anthropology and on human genetics. The present reviewer, a geneticist, was most impressed by the anthropological material, and cannot but wonder whether anthropologists may not react oppositely.

The present reviewer is not at all convinced by Gates' arguments, and believes that the unity of *Homo sapiens* can still be accepted. However, as Ernest Hooten has stated in the foreword, "The mere compilation of all this information in one volume results in a most useful reference work."—EDWARD O. DODSON, University of Notre Dame, Notre Dame, Indiana.

FUNDAMENTALS OF HUMAN REPRODUCTION. By Edith M. Potter, M.D. McGraw-Hill Company, New York. 1948. xi+231 pp., 92 figs. 12 plates. $3.50.

The story of human reproduction as developed in Dr. Potter's book is a concise, simple and accurate account of human embryology well suited to the needs of nurses' training classes for which it was written.

The beginning chapters of Part I introduce the student in a very generalized sort of way to the advent of living organisms on earth and to the structure and functions of the

typical cell as the fundamental unit of higher organisms. The evolution of the reproductive process is traced and the multiplication of individual cells is carefully outlined as well as the special preparation of the germ cells, through meiosis, to carry out their role in hereditary by the action of the chromosomes and genes.

In Part II a general foundation of anatomical knowledge of the adult male and female reproductive systems is laid down in preparation for a clear understanding of the functioning of the sex organs, and of the intricate relationships of the endocrine glands to the reproductive process in the female. This part also contains a good account of the early development of the blastocyst and the development of the extra embryonic membranes and placenta. A survey of the rates of intrauterine growth of the embryo during pregnancy concludes this section. It is followed by a group of excellent photographs illustrating early embryos.

The third section of the book includes discussions of the development of the various organs and organ systems of the embryo touching the high spots of each in a thorough and accurate manner.

The concluding section describes the process of birth and accompanying anatomical changes in the infant which follows its entrance into the outer world. The concluding paragraphs attempt to bring into proper relationship the role of heredity and environment in the further development of the individual.

On the whole, the book is admirably suited to its purpose of presenting the subject of human embryonic development to student nurses since considerable attention is paid to the reproductive process in the female and these have much practical interest to nurses.—F. B. ADAMSTONE, University of Illinois, Urbana, Illinois.

THE VERTEBRATE BODY. By Alfred Sherwood Romer. W. B. Saunders Co., Philadelphia. 1949. vii+643 pp., 363 figs. $5.50.

There has long been felt the need of a college textbook of vertebrate anatomy based on the comparative plan without special reference to the human, and the present book should satisfy this want. The opening chapter discusses the vertebrate body plan with brief considerations of symmetry, axiation, homology, the vertebrate organ-systems, and similar topics. The author cleverly evades getting himself entangled in the argument as to the meaning of the homology concept. The second chapter takes up prechordate types, including the hemichordates, now frequently relegated to the invertebrates, and after discussing the various theories of the invertebrate origin of vertebrates adopts the currently popular idea of an echinoderm affinity. The reviewer dislikes such coy titles as that with which the third chapter is labelled: "Who's who among the vertebrates." This ambiguous title covers brief descriptions of the various groups of vertebrates, including fossil ones, and is valuable as indicating the various lines of evolutionary ascent. The reviewer is puzzled by the inclusion of a chapter on cells and protoplasm, which certainly seems unnecessary in a book of vertebrate anatomy. The following chapter on vertebrate development presents the conventional accounts of cleavage, gastrulation, and germ-layer formation in the various classes of vertebrates but is freshened by the inclusion of colored diagrams of the fate of the various areas of early embryos. The remaining chapters (six to sixteen) take up in the usual order the various organ-systems with special emphasis on the author's specialities, the skeletal and muscular systems. There are two appendices, of which the first, giving a complete classification of the vertebrates, including the fossil groups, will be especially welcome.

The type is clear and readable, the illustrations neat and mostly labelled in full, and the style of writing easy on the gray matter. The text is not documented and there are no special bibliographies, only a list of general works. The reviewer finds both the color and design of the cover unpleasant.

This book very definitely caters throughout to the college level, which is to say, that it will be of very little value to teachers and advanced students of vertebrate anatomy. The reviewer feels a distinct dissatisfaction that a vertebrate specialist of Professor Romer's stature could not have given us more substantial fare.—LIBBIE HYMAN, American Museum of Natural History, New York.

AMERICAN SPIDERS. By Willis J. Gertsch. D. Van Nostrand Co., New York. 1949. i-xiii; 1-285 pages. 32 color plates, 32 gravures, 6 text figs. $6.95.

Most of the American books on spiders have been aimed at a taxonomic orientation of the group. In *American Spiders*, Dr. Gertsch has given a most attractive integration of biological information about spiders. From a competent background of knowledge and understanding of the entire group of arthropods, the writer throughout the book has woven a most fascinating web of explanations of relations of habits, structure and development of spiders in comparison with some of their better known relatives. Most of the chapters make intensely interesting reading.

The reviewer, from a speaking acquaintance with a local spider fauna gleaned from many years of amateur collecting, was at first unable to understand how the book could be of value in the hands of a student who has no background of first-hand experience with the taxonomy of spiders. This reaction soon gave way to a realization that the interesting and informative material has the possibility of instilling interest which may readily furnish the incentive for expansion of the student's inquiries into the systematic field.

The descriptions and narration are exceptionally free from stilted style and hackneyed expressions. The frequent reference to and quotations from mythology and folk lore add to the breadth of popular and cultural appeal. In deft strokes, many of the commonly mistaken beliefs, fears, superstitions and prejudices about spiders are wiped away. Fascinating facts and interesting information furnish a basis for an intelligent understanding and appreciation of the spider world.

The illustrations have highest scientific and artistic values. Excellent photographs from living specimens, most of them in natural surroundings, have replaced the customary drawings, except for a very few zinc etchings included as text figures to show analysis of details. A rapid scanning of the credit lines accompanying the plates gives evidence of the breadth of Dr. Gertsch's personal contacts with other students of spiders and with nature photographers. The natural color plates are especially good and add materially to the attractiveness of the volume. The jacket refers to "44 plates in full color and 67 in gravure," but these figures are not in agreement with the listing of plates cited on pages ix to xiii, nor do these numbers conform to the tally of individual figures in either of the series.

Against a book which has so many evidences of competent and meticulous professional preparation and careful embodiment of the skills of the book maker's art, it may not be amiss to voice one complaint as to its make up. The 32 plates in natural color and the 32 halftone plates are run in the text, but each series is numbered independently, the color plates in Arabic and the gravures in Roman numerals. In the intricacies of procedure and inflexible habits among publishers there might be some reason for this but to the reader it becomes confusing and annoying to have to look a second time to see if Plate Two is "Plate 2" or "Plate II," or is the latter an eleven? A single series of numbers for the plates would have avoided this potential confusion.

In this, the first of a new series to be known as *The Illustrated Naturalist*, a highly auspicious start has been made. In guiding the destiny of the series, the publishers have named an Editorial Advisory Board composed of William Beebee, Austin H. Clark, Robert Cushman Murphy and Fairfield Osborn. Such a board should be a guarantee as to the quality of succeeding volumes in the series.—HARLEY J. VAN CLEAVE, University of Illinois, Urbana.

THE PUPAE OF THE MOSQUITOES OF NEW GUINEA. By George Henry Penn. Pacific Science, The University of Hawaii, Honolulu, Hawaii. 1949. Vol. III, No. 1, pp. 3-85, 58 figs. $1.00.

Until recently the mosquito pupa has been somewhat neglected by taxonomic workers; however, the author has fully demonstrated in this publication that the pupal stage of the mosquito often has good differentiating characters. Sixty-eight of the 196 species of mosquitoes known to occur in New Guinea are included. The pupal stage of 36 species is described here for the first time.

In the discussion of "Features of Taxonomic Importance" (pp. 5-9) the morphology and chaetotaxy of the cephalothorax and abdomen are discussed. In designating pupal

setae the author follows the system used by Baisas with only slight modifications. This system involves a mixed terminology of letters, symbols and numerals. Table 1 shows the homologies of dorsal abdominal setae of mosquito pupae as designated by Macfie (1920), Senevet (1930), Baisas (1936 and 1938), Rozeboom and Knight (1946) and that of the author.

Pages 9 to 83 are given to "Systematic Treatment" which includes keys to subfamilies, genera, subgenera and species and descriptions of the genera and species. In general each species is described in the following order: References to earlier descriptions; Diagnosis; Cephalothorax; Abdomen; and Specimens Examined. Fifty-eight figures (line drawings) are included, four of which are generalized illustrations of taxonomic features of anopheline and culicine pupae while the remaining 54 figures are mostly of the dorsal aspect of the right half of the abdomen of species included in the study. The bibliography includes 50 carefully selected references.

The reviewer feels that this paper should be a valuable reference for those engaged in mosquito taxonomy and that it can be utilized as a guide for similar work in other areas.

Before closing the reviewer would like to call attention to another publication on this subject by Knight and Chamberlain, namely *A New Nomenclature for the Chaetotaxy of the Mosquito Pupa, Based on a Comparative Study of the Genera (Diptera: Culicidae)*. Proc. Helminthological Soc. of Wash., 15 (1): 1-10, 1948. This valuable contribution appeared too late to be included as a reference.—STANLEY J. CARPENTER, Fort Clayton, Panama Canal Zone.

A TEXTBOOK OF ENTOMOLOGY. By Herbert H. Ross. John Wiley and Sons, Inc., N. Y. 1948. ix+532 pp. $6.00.

Dr. Herbert H. Ross has produced a new *Textbook of Entomology* that seems to fill a vacant space in the series of texts that have been available. It is designed for the elementary student but makes the valid assumption that that student has a modicum of intelligence and likes to have his text arranged in a logical manner and give him a complete though not too detailed coverage of the entire subject.

After a short chapter on the history of entomology in North America the author proceeds to discuss the position of the Class Insecta in relation to the other classes of the Phylum Arthropoda and follows this discussion with chapters on the External Anatomy and Internal Anatomy. The more difficult subjects of Physiology and the Life Cycles are given somewhat more space in the next two chapters and lead easily into a treatment of the Orders of Insects.

This chapter, a little more than one-third of the book, opens with a key to the common orders which has been, perhaps, too simplified for the best interests of the student. The key is followed by short accounts of all the orders, both common and rare. In the case of a large order, a key to the common families is supplied.

The last three chapters deal with the Geological History of Insects, Ecological Considerations and Control Considerations. The basic facts of these subjects are well covered in a style that should prove interesting to the average student.

The book is well illustrated throughout, the letter press is excellent with a minimum of typographical errors and the binding is good. The reviewer regrets the fact that no mention of nomenclature is made. Even a beginning student should know something of the Law of Priority and the International Code of Zoological Nomenclature so that he will not be mystified upon discovering that many insects have had more than one name and that the acceptance of a name is by rule and not caprice. Also, it is probable that more extensive bibliographic references would add materially to the value of the text. Even so, the book is recommended for what it is, a beginning text in Entomology.—E. A. CHAPIN, U. S. National Museum, Washington, D. C.

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